Vol. 99. Part 1. Pp. 1-75. 21 figs. 15th March, 1948

COMMONWEALTH INST. OF ENTOMOLOGY LIBRARY
Eu-344
SERIAL SEPARATE

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGES

UVAROV, B. P., C.M.G., D.Sc., F.R.E.S.
Recent Advances in Acridology: Anatomy and Physiology of ACRIDIDAE . . . . . 1–75, 21 figs.

LONDON
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price £1 4*s.* 0*d.*

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1948-1949

C. B. Williams, M.A., Sc.D., *President.*
G. Fox-Wilson, N.D.H.
B. M. Hobby, M.A., D.Phil.
Miss C. E. Longfield
} *Vice-Presidents.*

A. Welti, *Treasurer.*

N. D. Riley, *Secretary.*

Other Members of Council.

E. B. Britton, M.Sc.
R. L. E. Ford.
R. M. Greenslade.
A. G. Hamilton, B.Sc., B.Agr., Ph.D., D.I.C.
Capt. R. A. Jackson, C.B.E., R.N.
H. B. D. Kettlewell, M.A., M.B., B.Chir., M.R.C.S., L.R.C.P.
A. M. Massee, D.Sc.
G. E. J. Nixon, B.A.
J. A. Simes, O.B.E.
W. H. Thorpe, M.A., Sc.D.
A. J. A. Woodcock, M.Sc.

Miss E. Evans, *Registrar.*

Finance and House Committee.

G. Fox-Wilson, N.D.H. (Chairman).

C. L. Collenette.
A. G. Gabriel.
H. E. Hinton, B.Sc., Ph.D.
Capt. R. A. Jackson, C.B.E., R.N.
A. M. Massee, D.Sc.

Publication and Library Committee.

W. H. Thorpe, M.A., Sc.D. (Chairman)

Prof. G. D. Hale Carpenter, M.B.E., D.M.
A. G. Hamilton, B.Sc., B.Agr., Ph.D., D.I.C.
G. E. J. Nixon, B.A.
J. Smart, B.Sc., Ph.D.
T. H. C. Taylor, D.Sc.

Committee on Generic Nomenclature.

Francis Hemming, C.M.G., C.B.E. (Chairman).

W. A. F. Balfour-Browne, F.R.S.E.
K. G. Blair, D.Sc.
O. W. Richards, M.A., D.Sc.
N. D. Riley (Secretary).

Committee for the Protection of British Insects.

H. M. Edelsten, O.B.E. (Chairman)

R. B. Benson, M.A.
E. A. Cockayne, M.A., M.D., F.R.C.P.
R. L. E. Ford.
B. M. Hobby, M.A., D.Phil.
Capt. R. A. Jackson, C.B.E., R.N.
Col. F. A. Labouchere.
A. M. Massee, D.Sc.
The Hon. Miriam Rothschild.
N. D. Riley (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Francis Hemming, C.M.G., C.B.E., appointed 1946.
   Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
2. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
3. **National Trust for Places of Historic Interest or Natural Beauty**
   Mr. H. M. Edelsten, O.B.E., appointed 1944.
4. **New Forest Association.**
   Mr. W. Fassnidge appointed 1934.
5. **New Forest Joint Committee.**
   Mr. W. Fassnidge, appointed 1939.
   Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.
6. **Royal Meteorological Society. Phenological Committee.**
   Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
7. **Council for the Promotion of Field Studies.**
   Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
8. **Joint Bioclimatic Committee.**
   Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
   Dr. C. B. Williams, M.A., D.Sc., appointed 1945.
9. **Yorkshire Naturalists' Trust, Ltd.**
   Mr. W. D. Hincks, M.P.S., appointed 1946.

RECENT ADVANCES IN ACRIDOLOGY: ANATOMY AND PHYSIOLOGY OF ACRIDIDAE.

By Dr. B. P. Uvarov, C.M.G., D.Sc.
(*Anti-Locust Research Centre.*)

Manuscript received 24th February, 1947.
(Read 4th June, 1947)

With Twenty-one Text Figures

CONTENTS.

		Page
	Introduction	2
I.	General Morphology	3
II.	Head	3
III.	Thorax	5
IV.	Abdomen	5
V.	Integument	6
	1. Histology, p. 6. 2. Colouration, p. 7. 3. Dermal glands, p. 7.	
VI.	Muscles	8
VII.	Digestive System	9
	1. Anatomy, p. 9. 2. Histology, p. 10. 3. Peritrophic membrane, p. 10. 4. Intestinal movements, p. 11. 5. Rate of digestion, p. 11. 6. Chemistry of digestion. p. 12. 7. Utilisation of food, p. 13.	
VIII.	Respiratory System	14
	1. Anatomy, p. 14. 2. Function of spiracles, p. 15. 3. Respiratory movements, p. 15. 4. Function of air-sacs, p. 16. 5. Regulation of respiration, p. 16. 6. Respiratory function of blood, p. 17.	
IX.	Circulatory System	17
	1. Dorsal blood vessel, p. 17. 2. Pericardial cells, p. 17. 3. Circulation, p. 17. 4. Blood, p. 18. 5. Respiratory function of blood, p. 20.	
X.	Excretory System	20
	1. Malpighian tubes, p. 20. 2. Rectal organs, p. 21. 3. Excretion, p. 21.	
XI.	Endocrine System	22
	1. Corpora allata, p. 22. 2. Corpora cardiaca, p. 23	
XII.	Oenocytes	23
XIII.	Nervous System and Sense Organs	23
	1. Central nervous system, p. 23. 2. Peripheral nervous system, p. 24. 3. Functions of the nervous system, p. 24. 4. Eyes and vision, p, 24. 5. Scolopophorous organs, p. 26. 6. Tympanal and other auditory organs, p. 27. 7. Brunner's organ, p. 30. 8. Prosternal tubercle, p. 31. 9. Krauss' organ, p. 31. 10. Various sensilla, p. 31.	
XIV.	Sound Producing Organs...	32
XV.	Reproductive System	33
	1. Male internal organs, p. 33. 2. Female internal organs, p. 34. 3. Male genitalia, p. 34. 4. Female genitalia, p. 36. 5. Gynandromorphism, p. 37.	
XVI.	Metabolism	38
	1. Chemical composition, p. 38. 2. Proteins, p. 39. 3. Fats, p. 40. 4. Chitin, p. 42. 5. Vitamins, p. 43. 6. Pigments, p. 43. 7. Gaseous metabolism, p. 46. 8. Water balance, p. 48. 9. Heat metabolism, p. 51. 10. Vitality, p. 58.	
	Bibliography	60
	Index to Species	74

INTRODUCTION.

When a general survey of the literature dealing with all aspects of knowledge on locusts and grasshoppers appeared some 19 years ago (Uvarov 1928a), the number of works on the subject published up to that time was estimated at about 2,000. Since then, a rapid development of research and of practical work on these insects has resulted in a great increase in the number of publications. A bibliography compiled and kept up-to-date by the Anti-Locust Research Centre includes nearly 2,500 titles of papers published on the subject since 1928 in some twelve languages. This bibliography is believed to be reasonably complete, except for popular articles, leaflets, etc., which are included only if they are found to contain original information. References to preliminary communications, when the results reported in them are published in full, are omitted. Papers dealing exclusively with the taxonomy of ACRIDIDAE are considered outside the scope of this bibliography, except those dealing with species of economic importance.

It would probably have been of value to those working on the locust and grasshopper problem if a mere list of titles were published, but it was thought that a digest of all published information, accompanied by full references to its original sources, would be more useful. The original intention was to review all publications since 1928 in a single summary covering all aspects of the problem, but this would involve a long delay. It was, therefore, decided to publish a series of summaries, each dealing with a special aspect of the subject, e.g. anatomy and physiology of ACRIDIDAE; development; ecology; control; etc. Apart from speeding up the publication, this arrangement will make it possible for a specialised student to find all data of interest to him in a conveniently concentrated form.

Since one of the main objects of these summaries is to assist acridologists in finding the required information, particular attention has been paid to collecting widely scattered data and those not readily accessible; such information is usually embodied in the summaries. On the other hand, larger papers containing abundant data are often merely referred to, since they must be consulted in the original.

In the hope that the summaries will not only help in research, but also stimulate it, considerable stress will be laid on pointing out the gaps in our knowledge which require to be filled. There are many problems in acridology which need investigation, some by laboratory students, others by field ecologists, and still others by practical workers. In this respect, all acridologists should be pleased to know that grasshoppers are becoming increasingly popular, particularly in the United States of America, as laboratory animals used for investigations of various general problems of physiology, development, etc. The results make for a better understanding of a living insect in its relations to the environment, and without such understanding there is little hope of finding a key to the locust and grasshopper problem.

The compilation of the bibliography and the preparation of the summaries would have been a formidable task, were it not for the ready co-operation of the many colleagues who greatly assisted the work by sending reprints of their papers, many of which might have escaped attention otherwise. These friends and helpers were so numerous that the present writer has to offer his apologies for thanking them all collectively, but none the less sincerely. It is only hoped that this and the following summaries will be of some use to them and to other workers, both as a source of information and as a stimulus.

Some errors and omissions in a work of this kind are unavoidable, and assistance in detecting them will be greatly appreciated. As a rule, papers published up to the end of 1946 have been included, but some earlier ones that appeared during the war years may be missing. Any additional references will be included in the general bibliography and the information used in the supplementary summaries which may be published later. The bibliography at the Anti-Locust Research Centre is maintained for the benefit of all acridologists and they can help to make it as complete as possible by sending copies of their own papers, and those published by others, for the library of the Centre. It would be particularly appreciated if two or more copies of each paper were sent, as this would make it possible to lend papers to field acridologists who have no access to libraries.

I. GENERAL MORPHOLOGY.

The best treatment of the external morphology, anatomy and histology of a single Acridid species is that by Jannone (1939e) who has dealt with *Dociostaurus maroccanus* in a most detailed manner, with very numerous illustrations. Karandikar's (1939, 1942) account of *Schistocerca gregaria* is less precise, and the same applies to the work by Sian (1935) on *Locusta migratoria* L. and by Lu & Chen (1928) on *Chondracris rosea* (called by them *Cyrtacanthacris flavicornis*).

It might be mentioned here, that some ACRIDIDAE (*Melanoplus, Romalea*) are now offered in zoological textbooks as more suitable examples of a generalised insect than the familiar cockroach. At least one British textbook (Whitfield & Wood 1935) includes a fairly detailed account of the external morphology and the internal anatomy of *Locusta migratoria*.

The external morphology of the separate parts of the Acridid body has been recently studied by several authors, but this information will be surveyed only very briefly, mainly in order to indicate the sources where exact morphological data can be found.

II. HEAD.

The normal type of head in ACRIDIDAE is hypognathous, i.e. with the frons more or less vertical and the mouth-parts directed downwards. Such a head is observed in most of the commoner species, such as

Locusta, *Melanoplus*, *Schistocerca*, etc. This type may be modified, the frons becoming more or less oblique, with the mouth-parts directed somewhat backwards (*Chorthippus*) ; or the head may be strongly elongated, the frons becoming almost horizontal (*Mesopsis*, *Radinotatum*, *Leptysma ;* see Salfi 1935) ; while an almost prognathous type of head is also known (*Euthymia*, *Hemiacris*). These specialisations of the head occur in taxonomically unrelated groups in connection with their habitats and habits.

Descriptions of the normal hypognathous head have been given by Snodgrass (1928 ; *Dissosteira carolina*) ; Chang (1931 ; *Gastrimargus marmoratus*) ; Chauvin (1938a ; *Schistocerca gregaria ;* very brief) ; and Karandikar (1939 ; also *S. gregaria*, but detailed and well illustrated). Snodgrass' treatment includes muscles as well and thus provides a basis for a study of modifications in head morphology in different groups of ACRIDIDAE ; such a study would be of great interest and of taxonomic value.

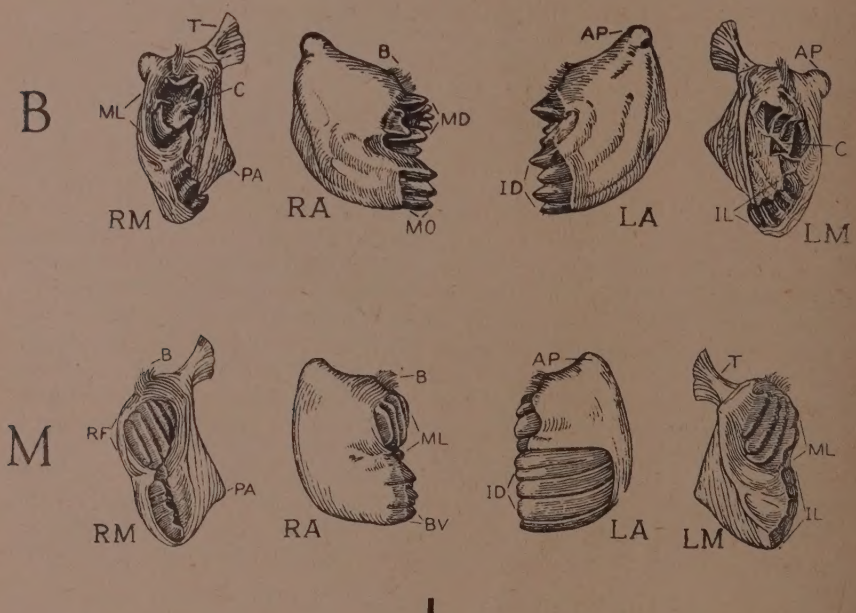


Fig. 1.—B, forbivorous mandibles of *Brachystola magna* (Girard) ; M, graminivorous mandibles of *Mermiria maculipennis* (Bruner).—RM, right mandible, mesal view ; RA, do., anterior view ; LA, left mandible, anterior view ; LM, do., mesal view ; MD, molar dentes ; ML, molar lobes ; C, concavities of molar areas ; ID, incisor dentes ; IL, incisor lobes. (*After* Isely 1944.)

As regards mouth parts, most interesting data on the morphology of mandibles have been published by Isely (1944). Two main types can be distinguished, one typical for species feeding mainly on broad-leaved plants (forbs in American terminology), and the other typical

of grass-feeders. Forbivorous mandibles (fig. 1, B) are characterised by the molar areas being provided with angular dents fitting into concavities of the opposite jaw, the whole forming an efficient masticating mechanism for the relatively soft leaves of forbs ; the incisor parts in mandibles of this type are acutely dentate, adapted for cutting. In graminivorous mandibles (fig. 1, M), the edges of the incisor parts are less jagged than in the forbivorous, and molar areas bear parallel ridges, which form grinding surfaces. In mixed feeders, intermediate structure of mandibles is found. Out of 89 species of North American ACRIDIDAE, 34 had graminivorous, 37 forbivorous and 18 herbivorous (intermediate) mandibles ; the first type prevailed amongst ACRIDINAE, while CATANTOPINAE were mostly forbivorous, and OEDIPODINAE mostly intermediate in the mandible structure. Further extension of such studies to members of other faunas and systematic groups is clearly promising. Other new data on mouth parts include a note by Rahman (1935) on the labium in *Locusta migratoria* and A. G. Hamilton's (1937a) description of an abnormal mandible in *Schistocerca gregaria*.

III. THORAX.

Snodgrass (1929) and Chang (1933) have published excellent monographs of the thoracic structures in *Dissosteira* and *Gastrimargus*, respectively, while Karandikar (1939) gave similar data on *Schistocerca* (see also Chauvin 1938a). Snodgrass' method of analysing sclerotised structures in connection with the muscles attached to them lends a new meaning to many details of structure, which used to be merely described. Thus, for example, several furrows on the sides of the pronotum correspond to ridges on the inner surface of the pronotum and serve for the attachment of muscles of the first pair of legs. Therefore, their disposition and degree of development has a definite functional importance, which opens up interesting prospects with regard to their study in relation to habits of various species.

Turning to the appendages of the thorax, the shape and structure of the hind femur and the armature of hind tibia present considerable variation in different ACRIDIDAE and their comparative study in taxonomically and ecologically different species should prove of interest.

IV. ABDOMEN.

In the past there has been considerable controversy with regard to the number of abdominal segments in ACRIDIDAE, and the latest view, that there are eleven (Snodgrass 1935 ; Roonwal 1937), is supported by the developmental history (Else 1934, Karandikar 1942). According to this interpretation the dorsum of the female abdomen terminates in the epiproct (or anal plate of taxonomists), which is the eleventh tergite (not the twelfth as stated in Uvarov 1928a) ; ventrally, the last segment

in the female is the eighth. In the male, the dorsal structure is the same, while ventrally the abdomen terminates with the enlarged ninth sternite (subgenital plate). The female ovipositor valves are usually regarded as appendages produced by the eighth and the ninth segments. There are three pairs of them, two pairs being strongly developed, while the third (interior) pair is small and concealed. Interesting abnormalities were found by Hamilton & Milnthorpe (1936) in three females of *Locusta migratoria*, in which an additional pair of ovipositor valves was produced by the eighth segment.

Further remarks on the structure of terminal abdominal segments will be given elsewhere (p. 35, 37).

V. INTEGUMENT.

1. *Histology.*

A thorough knowledge of the structure and properties of the Acridid integument is needed both for a better understanding of several important physiological problems (e.g. water balance, pigmentation, etc.), and for a sound approach to practical studies on the action of contact insecticides. Some work has been done in this direction recently.

Chauvin (1939b, 1941c) has dealt with the integument of *Schistocerca gregaria* in various stages of its development in a fairly detailed manner. Duarte (1939) described mainly the integument of the gut and Hollande (1940, 1943) studied protoplasmic structures in the gut epithelium. Brief data on the integument of *Anacridium aegyptium* have been presented also by Broussy (1933) in a paper dealing with pigments (p. 43).

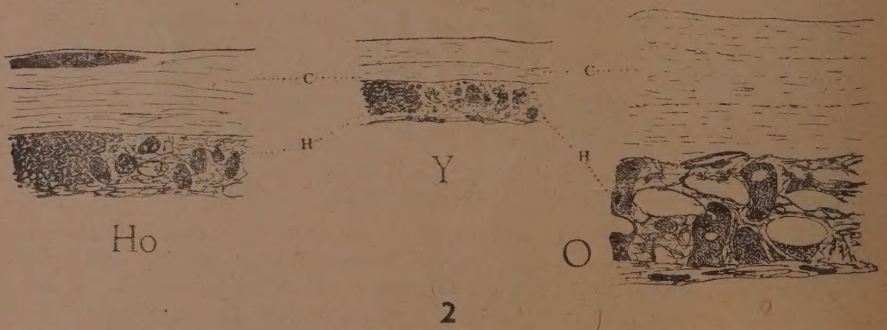


Fig. 2.—Integument of *Schistocerca gregaria*.—Ho, hopper of 5th stage; Y, young adult; O, old adult; C, cuticle; H, hypoderm. (*After* Chauvin 1941c.)

The integument consists of a single layer of hypodermal cells, and of a non-cellular cuticle (incorrectly called "chitine" by Chauvin). The cuticle consists of three layers: (1) thin outer membrane, or epicuticle which contains no chitin, but consists of a protein converted to sclerotin

and impregnated with lipids (Pryor 1939); (2) exocuticle, or the middle layer, also partly sclerotised; and (3) endocuticle.

The thickness of the cuticle and of the hypoderm vary in different parts of the body (Jannone 1939e), and both are also subject to changes during the development (fig. 2). The cuticle is supposed to be traversed by pore canals, but Duarte (*l.c.*) was unable to confirm this, possibly because of the technique used by him.

2. *Colouration.*

The cuticle and the hypodermal cells of the integument contain various pigments (p. 42) which are the cause of the general colouration and of its pattern. Both these features may depend on genetic factors, but they are also known to be liable to very considerable changes due to physiological processes during the individual development and to environmental influences.

Vorontsovskii (1928) made the first attempt to differentiate between genotypic and phenotyphic components of colouration and pattern, and he pointed out that a limited number of patterns recurs in various species of ACRIDIDAE. The whole series of pattern variations observed in one species may not be found in another, but the number of common patterns is greater in more closely allied species (Vavilov's rule of homologous series in variation (1922, *J. Genetics* **12**: 47-89)). Rubtzov's (1935) experimental studies showed the need for extreme caution in interpreting results of genetic work in colouration, since many components of the latter are subject to extensive phenotypic variation. Some geneticists, who attempted to study Acridid colouration (Sansome & La Cour 1935; Creighton & Robertson 1941) disregarded this possibility and their results lost some value accordingly.

All analytical, comparative, or experimental studies in colouration require, first of all, a comprehensive systematisation of its components. Clark (1943) has recently proposed a rational system for designating the more frequent pattern components and colours by letter-symbols, and it is to be hoped that this system will be followed and developed by future students of Acridid colouration.

3. *Dermal glands.*

The existence of some supposedly "defensive" glands in the thorax of *Oedaleus* has been noted before (Uvarov 1928a, p. 67), and now Jannone (1938a, 1939) has provided a very detailed account of an eversible glandular sac found in the prothorax of *Acrotylus* spp. The sac is present in all stages, from the first hopper to the adult, and when extruded it appears like a membranous vesicle exuding some fluid secreted by glandular cells. Experiments with a view to determining the stimuli causing the extrusion of the vesicle would be of interest and they may shed some light on the possible biological significance of this organ. The presence of a similar eversible sac in *Morphacris fasciata* has been recorded by Miller (1936, *Proc. R. ent. Soc. Lond.* (B) **5**: 158;

also Jannone 1939), and the organ is probably not confined to the three genera of OEDIPODINAE in which it has already been found, although Jannone reported its absence in *Locusta*, *Oedipoda* and *Sphingonotus*.

Similar structures, but in the first abdominal tergite, have been found in *Poecilocerus hieroglyphicus* and *Zonocerus* spp. belonging to the subfamily PYRGOMORPHINAE. The gland of *Poecilocerus* is a large bi-lobed sac extending the whole length of the first tergite and opening in the membrane between the first and the second tergite. From this opening a fluid can be ejected with some force. Properties of the fluid closely resemble those of the juice of *Calotropis procera*, the main food plant of *Poecilocerus* (Beier 1937).

Vacuolated glandular cells in the leg epidermis of *Melanoplus differentialis* were described by Slifer (Slifer & Uvarov 1938), but details of their structure and especially the existence of openings of their ducts remain to be studied and their function remains unknown. Cells of doubtful glandular nature were reported by Jannone (1939e) in the hypoderm of the intersegmental membrane in *Dociostaurus maroccanus*.

VI. MUSCLES.

The muscular system of ACRIDIDAE has been investigated in detail in a series of papers by Snodgrass. In the head, there are 45 different muscles (Snodgrass 1928), the most powerful ones being those moving the mandibles. A very complicated system of muscles exists in connection with other mouthparts, and there are muscles in the first two segments of the antenna, but not in the rest (see Imms 1940, for a diagram of antennal muscles in *Locusta*).

Muscles of the thorax are 94 in number, including the very complex system for the movement of legs and wings (Snodgrass 1929; see also Maki 1938, for a diagrammatic treatment of thoracic musculature in *Locusta migratoria* and *Atractomorpha ambigua*; and Uvarov & Thomas 1942, also in *L. migratoria*). In the abdomen 156 separate segmental muscles can be distinguished (Snodgrass 1935), apart from the transverse muscles which form the dorsal and ventral diaphragms functionally connected with the circulatory system. Muscles connected with the copulatory apparatus and the ovipositor have been studied by Guarino (1935).

The data on the relative weight of wing muscles in two species of ACRIDIDAE (Magnan and Perilliat-Botonet 1932) show that in *Oedipoda coerulescens* their weight was 8 per cent. of the total body weight, while in *Paracinema tricolor* it was 5 per cent. These figures are very low, since in a butterfly the muscle weight was found to be 22 per cent., and in a dragonfly (*Aeschna mixta*) even as high as 25·6 per cent. body weight, while in birds it varied from 2 to 35 per cent. Similar studies on good fliers among locusts would be of great value.

The physiology of Acridid muscles has been investigated by Solf (1931) by applying an electrical stimulus to isolated live muscles of the posterior femur. Muscles of *Anacridium aegyptium* showed a great

resistance to fatigue. It was not until after 1,000—1,400 repeated excitations (at the rate of one per second) that some reduction in the contraction was observed, and exhaustion occurred only after 3,000—4,600 excitations. The degree of contraction of a bundle was found to be 0·077 per cent. in the case of *Anacridium aegyptium* and 0·137 in *Prionotropis hystrix*. The same author also gave some data on the tetanus, and on the effect of temperature on muscular contraction. Lapique (1942) has studied the rapidity of the muscular response (chronaxie, as he called it) in normal and decapitated grasshoppers (not specified, possibly not ACRIDIDAE), as well as in the isolated posterior leg. Auger and Fessard (1928b) published some preliminary observations on rhythmic wing beating in *Locusta migratoria*, *Anacridium aegyptium* and an unspecified small grasshopper (Auger and Fessard 1929), caused by electrical stimulation of thoracic ganglia in decapitated insects.

As regards the biochemical side of muscle physiology, Means' (1942) studies suggest that neuro-muscular functions of *Melanoplus differentialis* depend on an acetylcholine-cholinesterase mechanism. Action of acetylcholine, atropine and nicotine on heart muscles in the same species was studied by H. L. Hamilton (1939) while Chauvin (1941c) reported the action of various substances on peristaltic movement of isolated intestine of *Schistocerca gregaria*. Respiration of the hind femur muscle in two species of *Melanoplus* was studied by Gilmour (1941).

VII. DIGESTIVE SYSTEM.

1. *Anatomy.*

Studies of the gross anatomy of the digestive tract have been published recently by Nenyukov and Parfent'ev (1929, *Locusta migratoria*); Pilat (1935, 1936, ditto); Snodgrass (1928, 1935, *Dissosteira carolina*); Hodge (1936, *Melanoplus differentialis;* 1939, *Locusta migratoria;* 1940, *Radinotatum carinatum;* 1943, *Leptysma marginicollis* and *Opshomala vitreipennis*); Stuart (1935, *Melanoplus differentialis*); Chauvin (1938, 1941c, *Schistocerca gregaria*); Chang (1931, *Gastrimargus marmoratus*, buccal cavity only, but treated in great detail); Atherton (1941, *Brachystola magna*, *Romalea microptera*). On the whole these studies serve only to confirm the data of previous workers (see Uvarov 1928a) and to suggest a great uniformity in the structure of the alimentary canal, at least in the representatives of three subfamilies—OEDIPODINAE (*Locusta*, *Dissosteira*, *Gastrimargus*), ACRIDINAE (*Radinotatum*) and CATANTOPINAE (*Schistocerca*, *Melanoplus*, *Brachystola*, *Romalea*, *Leptysma*, *Opshomala*). It remains to be seen whether variations can be found in other subfamilies.

The total length of the digestive tract in ACRIDIDAE has been considered relatively small (Uvarov 1928a), but this conclusion rested on measuring only the length of the intestine, without taking into account the gastric caeca which play an important part in the digestive process. When the aggregate length of the caeca is considered, the total length of the alimentary canal proves to be about three times that of the body

and the relative length of the mid-gut (with the caeca) is particularly noteworthy (Table I).

TABLE I.

Total Length of Alimentary Canal.

(After Nenyukov & Parfent'ev 1929; and Tareeva & Nenyukov 1931.)

	Locusta Hopper 4th stage	*Calliptamus* Adult female
Fore-gut	11 mm.	9·5 mm.
Mid-gut (with caeca)	30	62·5
Hind-gut	12	16
Body length	20	27
Ratio to body length	2·6	3·3

2. *Histology.*

The finer structure of the walls of the alimentary tract have received a good deal of attention from recent workers. The histology of its various parts in *Locusta migratoria* was described by Nenyukov and Parfent'ev (1929), Pilat (1935, 1936) and Hodge (1939), while Newell and Baxter (1936) investigated the structure of the free cell-border of the mid-gut epithelium in the same species. Woodruff (1933), Stuart (1935), Hodge (1936, 1937, 1939, 1940, 1943) and Hollande (1940, 1943) presented detailed data mostly on the finer cytology of the epithelial lining of the digestive tract while Beams and King (1932a) studied parietal cells of salivary glands. The development of the mid-gut epithelium in the embryo of *Melanoplus* has been studied by Stuart (1935a) and Riedel (1946) stressed that the connective tissue of the mid-gut is a feature deserving further study. Chauvin (1938, 1941c) described the histological structure of all parts of the alimentary tract in *Schistocerca gregaria*, and paid special attention to the pigmented cells which are present in the oesophagus, crop, gizzard and rectum, and thought them to contain a melanin; later (1939b, 1941c) he has rejected this conclusion, but reported melanin again in some cells of salivary glands.

3. *Peritrophic membrane.*

The question of the peritrophic membrane (a thin membrane enveloping the food mass in the gut) in ACRIDIDAE has only recently attracted attention. Woodruff (1933) considered the histological evidence for its presence in *Melanoplus* somewhat dubious and suggested that the membrane, if present, is not cellular, but consists of a secretory substance. Brown examined chemically the membrane enveloping pellets of excreta of *Melanoplus* and at first (1937) considered it to be non-chitinous, but on re-examination with different methods (1937a) concluded that it contains chitosan in pure form and is therefore almost certainly chitinous in nature. This was confirmed quite independently by von Dehn (1933) for *Stenobothrus* and by Berretta (1935, 1937) for *Anacridium aegyptium* and *Acrida turrita*, while Salfi (1937) obtained further evidence by examining isolated membrane in ultraviolet (Wood's) light and observing that its fluorescence resembled closely that seen in

the finest chitinous cuticle of the gut. Finally, Berretta (*ll.cc.*) presented histological evidence to show that the peritrophic membrane is formed in the anterior portion of the caeca, from a secretion and from the fusion

3

Fig. 3.—Isolated peritrophic membrane of *Anacridium aegyptium*. (*After* Berretta 1937.)

of protoplasmic and nuclear parts of their cells. This is well illustrated by the shape of a whole membrane which Berretta (1937) succeeded in isolating (fig. 3). The stratified character of the membrane suggests that its formation is a periodic phenomenon.

4. *Intestinal movements.*

Spontaneous peristaltic movements of an isolated intestinal tract of *Schistocerca gregaria* were observed by Chauvin (1941c) at temperatures about 40° C. Strong contractions were caused by barium chloride, but acetylcholine and histamin had no effect.

5. *Rate of digestion.*

The rate of digestion of food by ACRIDIDAE is relatively high. In the case of *Locusta* the food passes through the whole length of the alimentary canal in about an hour at a temperature of 32° C. (Nenyukov and Parfent'ev, 1929). Voskresenskaja (1936) feeding the insects of the same species after a long period of starvation, and dissecting them at intervals, has shown that 10 minutes after feeding, the whole fore-gut is filled and some food has reached the mid-gut; after one hour the whole canal is filled; after two hours no food remains in the fore-gut, but the whole canal is cleared only after about 9 hours. Tareeva and Nenyukov (1931) feeding *Calliptamus italicus* by food dyed with fuchsin and observing the appearance of coloured excreta, have found that *Polygonum* passes through the intestine in 2 hours 15 minutes, while wheat takes 2 hours 50 minutes, in both cases at 28° C. These results suggest that the rate of digestion depends on the kind of food and on the species of insect (as well as on the temperature).

A further interesting point has been raised by Monchadsky and Skoblo (*in* Predtechenskii 1935) who have established that the rate of passage of food through the alimentary canal of *Schistocerca gregaria* hoppers depends on the introduction of new food. While normally the food passes through the whole canal in 1½ hours on the average, in starving

individuals its passage is greatly slowed down ; after 3–4 days of starvation there is still some digested food in the mid-gut and hind-gut. This suggests some physiological regulation of the rate of digestion. Further research on this problem is needed, possibly with the use of the X-ray method used by Nielsen (1943) in his work on *Tettigonia*.

6. *Chemistry of digestion.*

The reaction of the intestinal content in four ACRIDIDAE studied by different authors was found to be acid in the fore-gut, and more or less alkaline in the mid-gut and hind-gut (Table II).

TABLE II.

Hydrogen ion concentration within the digestive tract.

Species	Fore-gut	Caecum	Mid-gut	Hind-gut
Locusta migratoria ... ... (Nenyukov & Parfent'ev 1929)	4·5	—	7–8	7–8
Calliptamus italicus ... ... (Tareeva & Nenyukov 1931)	5·2–6·0	—	7·2–8	7·2–8
Dissosteira carolina ... ... (Swingle 1931a)	6·10	6·66	7·31	7·01
Melanoplus femur-rubrum ... (Swingle 1931a)	5·48	—	7·48	6·00

Hastings and Pepper (1943) found the pH of the regurgitated digestive juices of six species of grasshoppers to range from 5·2 to 5·8. More detailed studies by Skrjabina (1936a), who applied electrometric method of pH determination, demonstrated, however, that the problem is a complicated one, since the value of pH in the mid-gut is subject to regular changes corresponding to stages in the digestion, as can be seen from Table III.

TABLE III.

Changes in the pH value in mid-gut during digestion.
(After Skrjabina 1936a.)

	Time after feeding.					
	5m.	10m.	1h.	3h.	6h.	12h.
Locusta	6·64	6·37	6·50	6·74	7·04	6·79
Calliptamus	6·39	—	6·48	6·75	6·96	6·67

It will be seen that the acidity of the mid-gut contents increases as soon as acid food reaches the mid-gut, but later the alkalinity increases probably owing to the secretion of digestive juice.

The results of determinations of digestive enzymes in *Calliptamus* made by Tareeva and Nenyukov (1931) ; in *Locusta* by Nenyukov and Parfent'ev (1929) ; in *Schistocerca americana* by Swingle (1931) and in *Stenobothrus* by Schlottke (1937) are presented in Table IV which shows

that the results obtained by different authors are somewhat divergent, possibly due to differences in methods, but they suggest a considerable similarity between the species studied.

TABLE IV.

Digestive enzymes in *Locusta* (L.), *Schistocerca* (S.), *Calliptamus* (C.), and *Stenobothrus* (St.).

	Salivary glands				Fore-gut				Caeca				Mid-gut				Hind-gut			
	L.	S.	C.	St.	L.	S.	C.	St.	L.	S.	C.	St.	L.	S.	C.	St.	L.	S.	C.	St.
Protease ...	−	−	+			−	−	+		+		+	+	+	+	+		+	+	+
Peptase ...	−		−				−	+				+	+		+	+			+	+
Lipase ...	+	−	+			−	−	+		+		+	+	+	+	+		+	+	+
Amylase ...	+		+			+	−	+		−		+	+	+	+	+		+	+	+
Cellulase ...	+			−			−	−				−	+		+	−			−	−
Lichenase								+				+				+				+
Maltase ...		−	−			+	−	+		+		+		+	+	+		+	+	−
Saccharase	+	−	+			+	−			+			+	+	+			+	−	
Inulinase ...	−		+				−						+		+				−	

Schlottke's (1937) studies on *Stenobothrus* were not restricted merely to proofs of the presence or absence of certain enzymes, but he determined also the concentration of each enzyme in different parts of the alimentary canal at different intervals after feeding. Enzymes in *Stenobothrus* are secreted practically continuously in all parts of the canal, with relatively little variation, while in carnivorous TETTIGONIIDAE there is a strong increase in their secretion when food is taken.

Chauvin (1938, 1939b, 1941c) recorded the presence of a special pigment in the cells of some sections of the intestine (*see* p. 43), but its physiological role remains obscure. The same author (1938e) submitted some evidence that oxidation of fats occurs in different parts of the intestine, but particularly at the level of the gastric caeca.

The cytological processes connected with the secretion of digestive juices were studied in *Melanoplus* by Woodruff (1933) and by Hodge (1936, 1937) and in *Anacridium aegyptium* by Hollande (1940, 1943). According to Woodruff the secretion is of the merocrine type, i.e. the secreting epithelial cells do not break down in the process. Hodge, however, believes that the secretion is, at least partly, of the holocrine type and even may be either merocrine or holocrine, dependent on physiological state.

7. *Utilisation of food.*

The important problem of the utilisation of food by ACRIDIDAE remains scarcely touched, but an interesting series of experiments was made by Brown (1937a) who fed *Melanoplus bivittatus* on artificial diets, consisting of finely chopped lettuce with the addition of a determined quantity of various carbohydrates. The amount of the carbohydrate in the excreta was estimated as a percentage of that consumed. The results showed that monosaccharides (glucose, galactose, xylose) are utilised completely, none being excreted. On the other hand, polysaccharides (inulin, dextrin, pectin) are passed through the alimentary

tract with practically no change. More surprisingly, the grasshopper proved to be unable to utilise starch grains (from potato and arrowroot). On the other hand, protein was entirely absent from the excreta, which suggests that it forms the chief nutritive substance extracted by the grasshopper from its food. Chauvin (1941c) criticised Brown's work because the latter did not study separately the excretion in the different stages of a grasshopper. Chauvin found that in *Schistocerca gregaria* the reducing sugars are retained particularly by hoppers and again by the sexually mature adults, while the maturing adults retained mostly proteins.

The effects of diet on development will be discussed elsewhere.

VIII. RESPIRATORY SYSTEM.

1. *Anatomy.*

Brief preliminary data on the whole respiratory system in *Brachystola magna* and *Romalea microptera* have been published by Atherton (1941).

Snodgrass (1929, 1935) presented a very detailed account of the structure of the thoracic and abdominal spiracles in *Dissosteira*. His treatment is particularly valuable because it includes a discussion on the closing mechanism, which varies substantially in different spiracles. Karandikar (1939) gave a good description and figures of thoracic spiracles in *Schistocerca gregaria*. The homology of Acridid spiracles with those of other Orthoptera was discussed by Amoroso (1936). A. G. Hamilton (1937) has supplied exact measurements of the length and width of the openings in different spiracles of *Locusta migratoria* (adults and 5th stage hoppers) and *Schistocerca gregaria* (Table V). These data refer, of course, to the openings between the sclerotised parts of spiracles, and represent the maximum values, which may be reduced even to zero by the action of the closing apparatus.

TABLE V.

Average measurements (in mm.) of spiracles in adults of *Locusta* and *Schistocerca* (after A. G. Hamilton 1937).

Spiracle No.	*Locusta*				*Schistocerca*			
	Male		Female		Male		Female	
	Length	Width	Length	Width	Length	Width	Length	Width
1	·813	—	·991	—	·940	—	·978	—
2	·559	—	·737	—	·711	—	·673	—
3	·300	·175	·376	·178	·394	·241	·445	·254
4	·315	·165	·363	·178	·317	·152	·394	·191
5	·215	·124	·241	·119	·229	·140	·203	·140
6	·173	·088	·211	·097	·165	·089	·179	·127
7	·153	·081	·178	·074	·152	·076	·152	·114
8	·142	·064	·178	·069	·152	·076	·152	·114
9	·145	·076	·191	·071	·152	·089	·152	·102
10	·268	·145	·320	·162	·279	·152	·292	·191

Apart from Jannone's (1939e) studies no work has been done recently on the tracheae except that A. G. Hamilton (1937) provided measurements of the diameter of the tracheae immediately adjoining each spiracle. A brief description of the tracheation of the tibia has been given by Friedrich (1929). The lack of new investigations on the air-sacs is particularly regrettable.

2. *Function of spiracles.*

As regards the function of the spiracles, McArthur (1929), McGovran (1931, 1932), Fraenkel (1932, 1932a), A. G. Hamilton (1937) and McCutcheon (1940), although using widely different methods, all arrived at the same conclusion that normally the first four pairs of spiracles serve for the inspiration and the last six pairs for the expiration; a different view of Koidzumi (1934–35) that all spiracles may be expiratory, was based on a faulty method (see p. 50). The normal procedure, however, is somewhat unstable, e.g. in an excited *Schistocerca gregaria*, all spiracles may open and close synchronously (Fraenkel, *l.c.*), and in *Melanoplus* the first four spiracles may sometimes serve for expiration (McArthur, 1929). The tenth pair in a flying *Schistocerca gregaria* serves for expiration, but in a resting locust it is inspiratory (Hamilton, *l.c.*).

3. *Respiratory movements.*

According to the usual conception, a normal respiratory cycle consists of alternating expiratory and inspiratory movements of abdomen, but Fraenkel (1932a) has noticed that the expiration consists of two phases, and McCutcheon (1940) has proposed to modify the scheme further by introducing a compressatory phase during which all spiracles are closed (fig. 4) and the air pressure in the tracheae and air-sacs is increased, thus

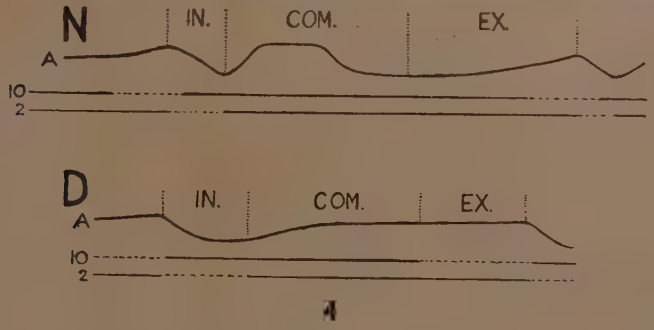


Fig. 4.—Normal (N) and dyspnoeic (D) respiratory cycle in *Dissosteira carolina*.—A, curve of vertical movements of the wall of 2nd abdominal segment; 10, tenth spiracle expiratory (solid line—closed; dotted line—open); 2, second spiracle, inspiratory (ditto); IN, inspiration; COM., compression; EX., expiration. (*After* McCutcheon 1940, modified.)

ensuring the penetration of air into the tracheoles. McCutcheon's theory is based on observations with the aid of ingenious apparatus and on measurements of air-pressure in different parts of the respiratory system and appears very reasonable. It is unfortunate, however, that his

discussion contains no reference to the earlier work by Fraenkel and Hamilton whose data cannot always be reconciled with McCutcheon's conclusions. McCutcheon has recorded only the vertical movements of the abdominal wall, although Fraenkel has pointed out that the respiratory movements include also the extension and contraction of the abdomen in length ; in a resting locust, the transverse and the longitudinal movements of the abdominal walls occur with a parallel rhythm, but in a flying one no longitudinal contraction takes place. It appears that respiration in a flying locust would correspond to the dyspnoeic type of McCutcheon in which the expiratory and the compressatory phases are merged. Chauvin's (1938b, 1941c) data on respiration in *Schistocerca gregaria* appear to confirm McCutcheon's conception.

The rate of respiratory movements is subject to variation. In a resting adult *Schistocerca gregaria*, the average frequency is 20 per minute according to Fraenkel (1932), and 40 according to Chauvin (1938b, 1941c) ; in the 5th stage hopper it is 60 ; in a flying adult it rises to 60–70. Great care, however, must be exercised in using such figures when studying the effect of external factors on respiratory movements, since even under constant conditions great variation, both in the frequency and in the amplitude of the movements, may be observed (Herber and Slifer 1928). For example, Kozhanchikow (1934) has recorded that in *Calliptamus italicus* the average frequency of respiratory movements remained 4 per minute at 20–35° C., at 40° C. it suddenly rose to 40, at 45° C. to 100, and at 55° C. to 160, but the figures are too irregular to be regarded as representing the influence of temperature on the rate of respiration.

4. *Function of air-sacs.*

According to Lee (1929) the air-sacs serve merely to increase the volume of air inhaled and exhaled during a respiratory cycle, but McCutcheon (1940) has suggested that the air-sacs permit the building up and retention of a sufficient pressure to supply air to the tracheoles. The importance of air-sacs for the internal temperature will be discussed elsewhere (p. 57).

5. *Regulation of respiration.*

In *Schistocerca gregaria* the respiratory movements are regulated by the thoracic ganglia and by those of the 5th and 8th abdominal segments. The thoracic ganglia are responsible for the rhythmic opening and closing of the thoracic spiracles which continue their movements even if the abdomen is cut off, so that the respiratory movements probably result from a rhythmic nervous activity (Fraenkel 1932a). On the other hand, we have seen above that not only the rate of respiratory movements but their whole sequence may be disturbed by handling, by a change in temperature, etc., which again suggests nervous responses. In addition, Fraenkel (*l.c.*) has suggested the existence of chemical regulation of respiratory movements and McGovran (1932) presented experimental data showing that the direction of tracheal ventilation may be reversed by the excess of carbon dioxide in the atmosphere. Thus, the available

incomplete data on the physiology of respiration suggest the necessity for great caution in applying experimental data to the interpretation of field observations. A living insect subject to numberless physiological and environmental influences, cannot be expected to function according to set formulae, and the respiratory processes appear particularly susceptible. The results for the insect may be far-reaching, since on them depends the rate of respiratory metabolism, intimately connected with the internal temperature, transpiration and water balance, which, in their turn, exercise a deep influence on the behaviour.

6. *Respiratory function of blood.* See p. 20.

IX. CIRCULATORY SYSTEM.

1. *Dorsal blood vessel.*

In *Dissosteira carolina* (Snodgrass 1935) and in *Schistocerca gregaria*, (Chauvin, 1941c) the dorsal blood vessel extends from the head into the tenth abdominal segment, and is provided with a pair of lateral openings (ostia) in each of the segments 2 to 9. In the mesothorax, metathorax and the first abdominal segment the blood vessel is supplied with dorsal ampullar enlargements. Snodgrass also gave a description of the muscles attached to the blood vessel, while Chauvin described histology of its wall in different stages.

2. *Pericardial cells.*

In *Schistocerca gregaria* groups of pericardial cells are attached to the outer covering of the dorsal blood vessel; they contain pigment (possibly, the same as in the cuticle, see p. 43) and protein crystals (Chauvin, 1941c).

3. *Circulation.*

The rate of heart beat in *Melanoplus differentialis* studied by Jahn, Crescitelli and Taylor (1937) varied from 40 to 70 beats per minute at 21–26° C. Electrocardiograms show that the nature of the heart-beats in the grasshopper is essentially similar to that in other invertebrates. The character of the beat was found to vary individually. In some of the grasshoppers the entire heart was observed to contract simultaneously, in others definite peristaltic waves of contraction progressed along the heart, usually commencing at the posterior end and passing forward. Isolated and excised portions of heart may continue to beat for some time. On the whole, it was concluded that a beat may be initiated anywhere, but that there are some controlling factors which normally co-ordinate the cardiac activity so as to produce a regular and synchronised beat (see also Crescitelli and Jahn 1938). The action of certain chemical substances on the heart beat was studied by H. L. Hamilton (1939).

The circulation of blood in the body remains unstudied. The circulation in the wings differs in hoppers and adults. In hoppers blood circulates not only in the peritracheal spaces along the wing-veins, but also between the two wing membranes; in adults, according to Guignon

(1936) the circulation is restricted to the peritracheal spaces round the wing-veins but the fact that black pigment is able to spread in an adult *Mesopsis* over the membrane (Burtt and Uvarov 1944) suggests that this is not always the case.

4. *Blood.*

The properties of the blood plasma of ACRIDIDAE remain almost unstudied. Its reaction was found to be mostly weakly acid in a number of North American species, the average pH values being 6·3–6·9, but there was a considerable variation not only between species (from 6·0 to 7·6) but also between different determinations in the same species (Boche and Buck 1942; Hastings and Pepper 1943). Russian writers found Acridid blood plasma weakly alkaline, the pH values being 7·1–7·3 in *Calliptamus italicus* (Tareeva and Nenyukov 1931; Skrjabina 1936a), 7·29 in *Locusta migratoria* and 7·39 in *Dociostaurus maroccanus* (Skrjabina, *l.c.*). The buffering capacity (ability to resist changes in reaction upon the addition either of an acid, or of a base) of the plasma was found to be weak in the few species studied by Hastings and Pepper (1943). No investigations on the composition of plasma are known, except Blumenthal's (1927) determinations of the sugar content in five species where it fluctuated from 30·6 to 49·4 mgr. per 100c.c. Further more detailed and more exact work on blood plasma and its variations in connection with sex, age, instar, phase, etc., are obviously needed.

The available data on the cellular elements of the blood are better than those on its plasma. In *Calliptamus italicus*, Tareeva and Nenyukov (1931) distinguished three kinds of blood cells. Pilat's (1935a, 1936a)

5

Fig. 5.—Haematocytes of *Schistocerca gregaria*.—A, mother cell; B, do., dividing mitotically; C, pro-leucocyte; D, leucocyte with lobed nucleus; E, phagocyte; F, mother cell with supposed pseudopodia. (*After* Mathur & Soni 1937, modified.)

work on *Locusta migratoria* has confirmed the view of some previous authors (working on insects other than ACRIDIDAE) that the cells of different size, shape and properties found in the blood are merely stages

in the development of one type of cell. The series begins with small globular haematocytes, about 8–9μ in diameter, in which the nucleus constitutes the main mass of the cell, the cytoplasm being represented by a narrow layer round the nucleus. These " mother-cells " (as they have been called by later investigators) gradually increase in size, mostly by the growth of the cytoplasmic layer. Such large haematocytes possess a power of amoeboid movement by forming pseudopodia, though Mathur and Soni (1937) working on *Schistocerca gregaria* maintained that no amoeboid movement occurs at any stage. But on exposure to air structures resembling pseudopodia result from plasmolysis. The last named authors described the mitotic division of the mother-cells, which may result in two spindle-shaped pro-leucocytes (fig. 5). When a pro-leucocyte has grown to its full size, its cytoplasm may assume a granulated appearance because of the swelling of the mitochondria, and the cell becomes a leucocyte ; alternatively, a pro-leucocyte in which the mitochondria retain their original size becomes a phagocyte. These two types are almost exactly alike in shape and size (up to 40μ long and 16μ wide), but the granular leucocytes possess no phagocytic properties. The data of Mathur and Soni were largely confirmed by Lepesme (1938) on the same species of locust.

Apart from the cellular elements just described, the blood contains fat globules and muscle fibres in different stages of disintegration, as well as degenerating blood cells.

Tauber and Yeager (1935) provided a series of the total counts of cells in the blood taken from antennae (Table VI) of different ACRIDIDAE.

TABLE VI.

Total cell counts in a cubic mm. of blood (after Tauber & Yeager 1935).

Species	Stage	Range of counts	Average
Melanoplus femur-rubrum	Adults	13,278—16,889	15,023
M. spretus	Adults	18,881—32,498	24,534
M. differentialis	Adults	19,547—27,440	23,509
Do.	Hoppers	15,860—17,240	16,550
M. bivittatus	Adults	32,573—41,828	38,243
Dissosteira carolina	Adult♂	35,910—36,158	36,034
Do.	Adult♀	53,408—61,320	56,033
Arphia sulphurea	Adult♂	14,663—18,075	16,348
Do.	Adult♀	— —	22,588

The table shows that the total number of cells per cubic millimeter is variable and may be nearly twice as great in one individual of the same species as in another. Nevertheless, some figures for different species diverge so widely as to suggest possible specific differences. In the two cases when sexes were studied separately, the figures for females were definitely greater than for males. Data on hoppers show a considerable increase in the number of cells in the adult as compared with the hopper. In a few cases, not included in the table, individuals parasitised with nematodes showed abnormally high cell numbers, suggesting

that the latter may be due to a pathological condition. This makes it probable also that high numbers in females may be associated with oviposition periods, but unfortunately no data on the state of gonads is given.

Mathur and Soni (1937) who have studied the blood cell numbers in all stages of development of *Schistocerca gregaria* obtained figures so widely divergent from those given by Tauber and Yeager that some doubts arise as to whether they have counted all blood cells, or only certain types of them. In the young adult (sex not stated) the Indian authors found only 6,000–6,500 cells per cub. mm. of blood taken from the cervix. In the first stage hopper the average number was 220 ; in the second 390 ; in the third, 1,180 ; in the fourth, 3,000 ; and the fifth, 5,000. Thus the number of blood cells rises with each stage, while parallel with it the number of fat globules, which are very numerous in the first stage hopper, steadily decreases with the development. In the adult they almost disappear. This suggests that fat globules are being utilised during the hopper development.

These data on the blood cell numbers, although only preliminary and probably inexact, suggest that it would be of value to study the variation in the number of cells in relation to the taxonomic position of the insect, as well as during the various periods of its development ; during different seasons ; in individuals subjected to different external conditions, etc.

5. *Respiratory function of blood.*

The blood of *Locusta migratoria* and *Anacridium aegyptium*, according to Kreps and Chenykaeva (1942, 1942a), contains no carbon anhydrase, the enzyme which in vertebrates takes part in the reversible reaction $CO_2 + H_2O \rightleftarrows H_2CO_3$ connected with transportation of carbon dioxide by the blood. The Acridid blood contains, however, another substance which inhibits hydration of carbon dioxide, but not its dehydration. This substance remains unknown, but it is not an enzyme, being thermostable and resistant to the usual enzyme poisons. Its presence in insect blood prevents the free CO_2 from being transformed into H_2CO_3 and free gas molecules of CO_2 may be more easily discharged through tracheae and directly through the integument. Confirmation of this work is required.

X. EXCRETORY SYSTEM.

Brief preliminary data on the excretory system in *Brachystola magna* and *Romalea microptera* have been published by Riedel (1941).

1. *Malpighian tubes.*

Stuart (1935) has presented a good anatomical and histological description of Malpighian tubes in *Melanoplus differentialis*. In this species they are 190–300 in number, divided into an anterior group of tubes directed forward and extending as far as the gastric caeca, and a posterior group extending backward to the rectum. They are grouped

into twelve bunches, each of which opens into an excretory ampulla placed on the digestive tube just anterior to the ileoventricular sphincter. There are thus twelve ampullae, each receiving 6–10 of the anterior tubes and 10–16 of the posterior ones. A single Malpighian tube consists of a single layer of large polygonal cells, covered externally by thin and flat " peritoneal " cells and internally by a striated border similar to that in the mid-gut. The inner wall of the mid-gut is gathered into twelve folds, separated by deep " excretory furrows." Each of these furrows continues into the lumen of an excretory ampulla. Chauvin (1941c) described briefly the histology of Malpighian tubes in *Schistocerca gregaria* and their connection with the dorsal blood vessel.

Lison (1937, 1937a, 1938) working mostly on cockroaches and earwigs, but also on a grasshopper, *Chorthippus bicolor*, proved that cells of Malpighian tubes are able to absorb and accumulate in their protoplasm certain acid colouring matters, but not the diffusible ones.

Drilhon & Busnel (1939 ; Busnel & Drilhon 1942 ; Drilhon 1943), suggested that Malpighian tubes may have not only an excretory function, since in *Schistocerca gregaria* they were found to accumulate flavin, a substance containing vitamin B_2, in quantities up to 0·00215 per cent. of the weight of fresh tissue. Gourevitch (1937) found the flavin content of this locust to be 0·000025 per cent. of live weight.

2. *Rectal organs.*

The anatomy and histology of the so called " rectal glands " has been studied in *Locusta migratoria* (Nenyukov & Parfent'ev 1929), *Melanoplus differentialis* (Hodge 1936), *Radinotatum carinatum* (Hodge 1940), and *Melanoplus femur rubrum* (Marshall 1945). According to the last named author who reviewed the literature on the subject, there are six glands, one ventral, one dorsal and two lateral ones on each side. The epithelial cells in the glandular region are large, columnar, covered on the inner surface by thin cuticular intima and provided by a striated border. A feature of the cells is the presence of two types of nuclei, the larger and the smaller ; the smaller nuclei are sometimes surrounded by a vacuole from which a duct leads into the lumen of the rectum. Thus, there is a suggestion of glandular function of rectal organs, though the use of secretion so near the posterior end of the intestine is not clear. The abundance of tracheae in the epithelium of rectal glands must have some physiological meaning (Nenyukov & Parfent'ev 1929 ; Marshall 1945), but no explanation is yet available. Wigglesworth (1939) suggested that rectal organs may serve for the absorption of water from the faeces, but Snodgrass (1935) opposed this view.

3. *Excretion.*

Brown (1937) has studied the excreta of *Melanoplus bivittatus* fed on an exclusive diet of lettuce head. The excretory pellets are oblong, ellipsoid in shape, up to 3–5mm. in length, and vary in colour between red, brown and black. Their surface is wrinkled, because of a thin covering formed by the peritrophic membrane (p. 10). Included within

the membrane are the undigested food residues, impregnated with urinary constituents ; some of the latter also form encrustations in crystalline form on the outside of the membrane. Chemical analysis showed that uric acid is the predominant substance. Urea, amino-nitrogen, arginine and phyllobombicin were also found in the excreta.

Chauvin (1941c) working on *Schistocerca gregaria* pointed out considerable variation in the chemistry of excretion between different stages of the insect. The excretion of a hopper and a sexually mature adult is similar, but an immature adult excretes more urea, uric acid and sugars (Table VII).

TABLE VII.

Percentage composition of excreta of *Schistocerca gregaria* in different stages (after Chauvin 1941c).

	Hoppers		Adults	
	4th stage	5th stage	Immature	Mature
Total nitrogen	1·61	1·36	1·855	1·575
Soluble nitrogen	0·56	1·05	1·61	0·78
Ammonia	0·2048	0·2652	0·72	0·4692
Urea	—	—	0·50337	—
Uric acid	1·008	1·092	2·35	1·176
Cholesterol	—	0·0026	0·0015	0·0008
Sugars	—	1·49	2·75	0·93

It will be seen that recent contributions to the study of the excretory system and excretion in ACRIDIDAE are very modest, and cannot in any way be considered commensurate with the great importance of this function in the insects' economy.

XI. ENDOCRINE SYSTEM.

1. *Corpora allata.*

Until relatively recently the corpora allata, a pair of " small, compact, cellular bodies, generally oval, elliptical, or spherical in form, lying at the sides of the stomodaeum behind the brain " (Snodgrass 1935a), have been regarded as belonging to the " sympathetic " nervous system (Uvarov 1928a, fig. 15c, S ; see below, p. 23). Histological studies have now shown that although the corpora allata are of ectodermal origin, they do not consist of nerve cells. Their structure in *Locusta migratoria* and *Anacridium aegyptium* has been studied by de Lerma (1937), and in *Chorthippus bicolor* and *Mecostethus grossus* by Hanström (1940), and these authors definitely suggested that corpora allata function as glands of internal secretion. Experiments with *Melanoplus differentialis* performed by Weed (1936, 1936a ; Weed Pfeiffer 1939, 1945, 1945a) proved that corpora allata produce a metabolic hormone which is essential for the production, or mobilisation, of materials necessary for egg production. Full data on the subject should be more appropriately treated in a summary dealing with development of ACRIDIDAE, and it

is sufficient here to state that the removal of corpora allata from females resulted in a reduction of water content (see p. 48), and in a great increase of fat content (see p. 40) ; the development of eggs was inhibited and so was the secretion in oviducts. On the other hand, no effect of corpora allata on moulting, as in the case of other insects, was observed. Hanström (1936, 1938, 1939, 1940, 1940a) injected extracts of the heads of five species of ACRIDIDAE into the crustacean *Leander adspersus* and observed strong contraction of the chromatophores, such as is observed under the action of a special hormone secreted by the crustaceans themselves ; the extract may have contained a hormone, secreted by the corpora allata, which is possibly connected with colour changes in these insects.

2. *Corpora cardiaca.*

In *Locusta* and *Anacridium* the corpora cardiaca (pharyngeal bodies) are a pair of small elongate structures lying on the dorsal side of the pharynx and partly fused with each other (see p. 24). Histologically they are characterised by the presence in their distal ends of glandular cells which are in contact with the dorsal vessel and with the haemolymphatic lacunae of the head. This suggests their probable endocrine function (de Lerma 1937 ; Hanström 1936–1940a).

XII. OENOCYTES.

Since the function of oenocytes remains a matter of surmise, it appears best to treat them not in connection with any system of organs.

Oenocytes are special large cells which, e.g. in *Schistocerca gregaria*, are disposed in groups near the abdominal spiracles and generally along the two main abdominal tracheal trunks (Chauvin, 1937, 1938d, 1941c). In *Locusta migratoria* nymphs they are also found in contact with tracheae, as well as in the fat-body and hypoderm (Duarte 1939). Chauvin proved the presence in oenocytes of a pigment apparently related to lipochroms, which are products of the oxidation of fats, and suggested that oenocytes play a part in the metabolism of fats, by absorbing them from the fat-body, while oxygen is absorbed from the tracheae. On the other hand, it has been suggested for other insects and reiterated by Duarte for *Locusta migratoria* that oenocytes may have a secretory function connected with moulting.

XIII. NERVOUS SYSTEM AND SENSE ORGANS.

1. *Central nervous system.*

Snodgrass (1935a) and Nesbitt (1941) produced detailed illustrated descriptions of the central nervous system and particularly of the brain in *Dissosteira carolina*, but it would be impossible to summarise the data here. The stomatogastric nervous system (sometimes called the sympathetic, or stomodaeal) has also been described by these authors (*ll.cc.*) and by de Lerma (1937 ; *Anacridium aegyptium*), while the latest treatment of this system in *Schistocerca americana* belongs to Bickley

(1942). The system consists of a frontal ganglion lying just above the pharynx and connected by the recurrent nerve with the occipital ganglion, to which are attached paired corpora cardiaca (pharyngeal bodies). Below the occipital ganglion, and also connected with it by short nerves, are a pair of corpora allata. Extending posteriorly from the occipital ganglia are two pairs of nerves; one pair soon branches along the oesophagal wall and sends fibres to the aorta; the other (oesophagal nerves) runs along the crop and ends in the ingluvial ganglia. For the histology of ganglia, *see* Bruno (1931), Beams & King (1932), and Jahn and Wulff (1942a).

2. *Peripheral nervous system.*

The data on the peripheral system are very scanty (Nesbitt 1941; brief data on the nervous chain). An interesting account of the innervation of wings of *Chorthippus biguttulus* (L.) is provided by Zacwilichowski (1934, 1934a) Friedrich (1929) has described the nerves in the tibia of several grasshoppers and Slifer (1935) those in the femur, though in both cases the descriptions are not complete, since they were made in connection with studies on the innervation of the chordotonal organs (p. 27). Nerve endings in muscles of *Elaeochlora*, as described by Jorg (1933) are of two kinds – simple branching endings, and more complicated, anastomosing structures ending in plates.

3. *Functions of the nervous system.*

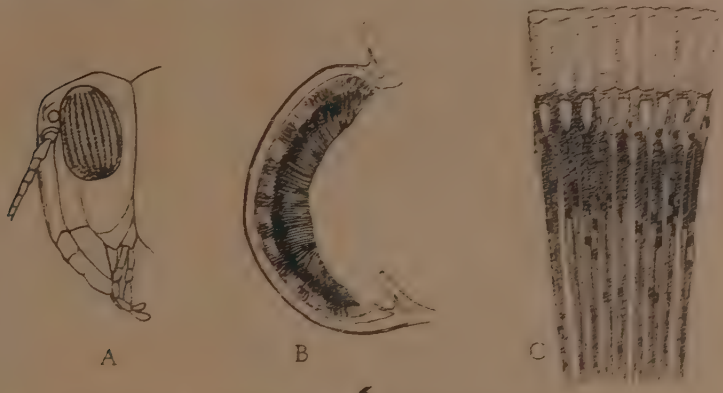
Auger and Fessard (1928, 1929) reported on some experiments on the electric excitation of the central nervous system in *Anacridium aegyptium* and *Locusta migratoria*. On inserting one electrode into the visceral ganglion and bringing another into contact with the nervous chain of a decapitated insect, vibrations of the wings and elytra, as well as contractions of the legs, were observed.

Other experimental work, bearing on the perception of stimuli, and on the insects' reactions to them will be reviewed under the respective sense organs and in the summary dealing with behaviour.

4. *Eyes and vision.*

Friza (1929) was the first to investigate the morphology of the compound eyes in ACRIDIDAE which often show a dark pattern on a lighter background. Thus, in *Anacridium aegyptium*, the eyes have 8-9 vertical dark stripes (fig. 6). The same pattern has been more recently recorded in *Schistocerca gregaria* (Roonwal 1936a; Mukerji & Batra 1938; Volkonsky 1938b, 1938c), in which the number of stripes in the adult varies from five to eight. The stripes cross the whole eye except for a small uniformly dark area at the upper end, called the "dorsal spot" by Roonwal (*l.c.*); this area is separated from the rest of the eye by a distinct pale line. In a section, it can be seen that each ommatidium is enclosed in a sheath of pigment cells, but the cells contain pigment only in the dark portions of the eye. The physiological significance of the stripes is not clear. Friza has suggested that the stripes serve to

isolate groups of ommatidia and prevent the influence of the obliquely falling light rays, which may increase the sensitivity of ommatidia to



6

Fig. 6.—Pigmentation of compound eye in *Anacridium aegyptium*.—A, striped pattern of the eye; B, transverse section of the eye, showing stripes; C, do., greatly enlarged. (*After* Friza 1929.)

the rays falling in the direction of their axes and thus play a part in the orientation of the insect to light.

Striped eyes are also found in *Calliptamus italicus* (Friza, *l.c.*), *Catantops*, *Acrida*, *Caloptenopsis* (Rao 1938b), *Thisoicetrus littoralis*, *Schistocerca paranensis* (Volkonsky, 1938b), *Patanga succincta*, *Cyrtacanthacris tatarica*, *Hieroglyphus banian*, *Spathosternum*, *Dericorys* (Rao & Gupta 1939), all these being insects living in fairly dense vegetation. On the other hand, *Sphingonotus coerulans* and *Oedipoda coerulescens* living mostly on bare ground have the eyes spotted with round dark spots (Friza, *l.c.*). In *Psopha stridula* the whole lower half of the eye is black, while the upper is light grey (Friza, *l.c.*); this species lives in short grass and is usually exposed to strong insolation. Some correlation, therefore, appears to exist between the type of eye pattern and the ecology of species, and further studies in this direction may throw some light on the biological meaning of the pattern. In genera of PYRGOMORPHINAE (*Pyrgomorpha*, *Colemania*, *Chrotogonus*) the stripes are not vertical, but concentric; this may well be a taxonomic character.

The average number of facets in a compound eye of adult *Schistocerca gregaria* was estimated by Bernard (1937) as 9,400, the average diameter of a facet being 27·5μ.

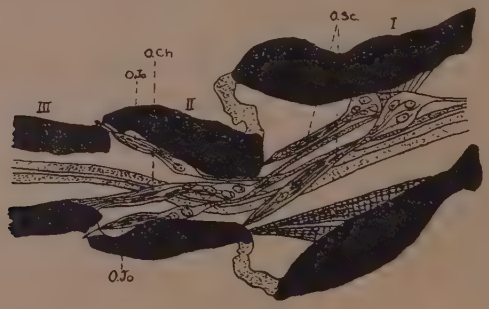
Studies in the physiology of vision are only beginning and results so far published refer mainly to the adaptation phenomena. The electro-retinograms obtained from grasshopper eye are qualitatively similar to those of a vertebrate eye. A dark-adapted eye of *Melanoplus differentialis* responds to brief flashes of light by a simple wave consisting of a rapidly rising limb and a slowly descending one; light-adaptation results in a wave consisting of two distinct phases (Hartline 1928; Jahn & Crescitelli 1938; Jahn & Wulff 1942; Taylor & Crescitelli 1944).

In addition to these retinal responses, oscillatory electrical after-discharges were found to occur under conditions of continuous illumination; they are considered to have their origin in the optic ganglion (Crescitelli & Jahn 1939a, 1942; Roeder 1939, 1940; Jahn & Wulff 1942a). The magnitude of electrical response varies with temperature (Jahn & Wulff 1942) and the appearance of oscillations is connected with the temperature range of 27°–42° C. (Crescitelli & Jahn 1939a) The response varies with the light intensity but not with its wave-length, the effect of different coloured lights depending only on their relative intensities (Crescitelli & Jahn 1939; Weiss 1944). While in some insects there is a distinct diurnal rhythm in the eye responses, no such rhythm was found in *Melanoplus differentialis* (Jahn & Crescitelli 1940). Although the experiments involved only some half-dozen species of grasshoppers, significant specific differences in the responses were observed (Hartline 1928; Jahn & Wulff 1942, 1942a; Taylor & Crescitelli 1944), and further extensive work on species widely differing in their ecology should be of great interest. In view of the known importance of vision in behaviour (Kennedy 1939), research on the physiology of vision is urgently needed.

5. *Scolopophorous organs.*

One of the most widely spread types of sense organ in insects generally is the scoloparium, or scolopophore, consisting of a group of special nerve cells called scolopalia, or sense rods. These organs have sometimes been called chordotonal, because they used to be regarded as receptors for vibrations, which proved to be true only in certain cases, while the function of the vast majority of scolopophores remains entirely unknown.

Slifer (1936) has studied the scolopophorous organs of *Melanoplus differentialis*, and presented a list of 76 pairs of such organs, scattered



7

Fig. 7.—Longitudinal section of three basal antennal segments (I, II, III) in *Schistocerca gregaria*, showing Johnston's organ (O. Jo.), chorodotonal organs in the first (O. Sc.) and in the second (O. Ch.) segments. (*After* Debauche 1938.)

over practically every part of the body, except the wings. This exception is of interest, since scolopophores are known to occur on the wings of BLATTIDAE, and their absence in ACRIDIDAE (and in saltatorial Orthoptera

generally) may have a phylogenetic significance (Zacwilichowski 1934).

While the great majority of scolopophorous organs consist only of a few nerve cells and have been merely recorded, others are more complicated and have received special names. Thus, inside the first two antennal joints of many insects, including ACRIDIDAE, there are found groups of scolopalia forming distinct organs. In the first joint, there is a pair of scolopophorous organs, extending from the inner wall near the base to the base of the second joint. The second joint itself contains the, so-called *Johnston's organ* (fig. 7). This consists of forty groups of elongated scolopalia, arranged in a cylinder round the periphery of the joint and attached by their distal ends to the membrane between the second and the third joint. In addition to Johnston's organ, the second antennal joint has yet another scolopophorous organ extending obliquely along the middle (Debauche 1938, *Schistocerca gregaria ;* Jannone 1939e, *Dociostaurus maroccanus ;* Eggers 1928, summary). There is no definite evidence as to the function of the antennal sense-organs, but their structure and arrangement suggest that they may serve for recording the movements of the antennae, which are known to possess other sense organs stimulated by various external factors.

Another relatively well-known kind of scolopophore is represented by the *chordotonal organs* in the legs of ACRIDIDAE. In the femur, an organ of this kind extends almost throughout its length and its sensory portion is divided into two groups of scolopalia (Slifer 1935). Tibial organs are three in number, one being close to the base of the tibia, just under the knee (subgenual organ) ; one a little lower down ; and one in the apical quarter of the tibia (Eggers 1928 ; Friedrich 1929 ; Debaissieux 1938). Scolopophorous organs are found also in the tarsal joints of ACRIDIDAE (Debaissieux 1938). The function of these organs in the legs remains wholly obscure, though recent studies of Pringle (1938, *J. exper. Biol.* **15 :** 101–131 ; 467–473), on the analogous organs in cockroaches suggest that they may serve to record the pressure and the stresses on the cuticle, and may therefore play an important part in maintaining the position of the legs and of the whole body.

6. *Tympanal and other auditory organs.*

The tympanal organs also belong, by the structure of their nerve cells, to the category of scolopophores, but deserve a separate discussion owing to their complexity and their proven auditory function.

The classical description of the tympanal organ in ACRIDIDAE by Schwabe (see Uvarov 1928a ; Schumacher 1937 ; Eggers 1928, summary) has been confirmed for *Schistocerca gregaria* by Hers (1938).

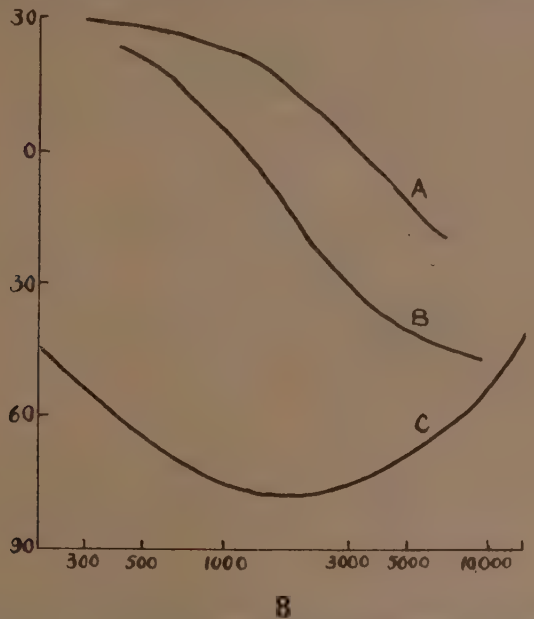
Knetsch (1939) made an interesting, if somewhat superficial, attempt to survey the variation in the structure and development of tympanal organs in various subfamilies of ACRIDIDAE. The relative size of the tympanum is very variable. The total body length is 51·78 times the diameter of the tympanum in *Chrotogonus* and only 10·98 in *Prionotropis*, i.e. the latter has the tympanum five times as large relatively as the former. The size varies also with the sex, females usually having smaller

tympana. An important external feature of the tympanal organ is a fold of its chitinous rim which may vary greatly in development. In the simpler cases the tympanum is on the level of the integument and the rim is not raised (PAMPHAGINAE, PYRGOMORPHINAE) ; specialisation consists in the tympanum becoming sunk in a depression and the rim expanding into a shell-like covering (ACRIDINAE, OEDIPODINAE, CATANTOPINAE). The development of the tympanal cover is variable and in *Stenobothrus* species, for instance, the tympanum is almost completely covered, there being only a narrow slit leading to it. As a rule, the covering is more complete in males. Further variations occur in the sense organs found on the inner side of the tympanum. In the most specialised forms with large covered tympana (ACRIDINAE, OEDIPODINAE and CATANTOPINAE) the organs consist of four separate bodies, in *Paulinia* there are only three bodies ; in PAMPHAGINAE two ; and in PYRGOMORPHINAE only a single sensory body. All these variations in the tympanal organs are correlated with the development of stridulating organs and of the wings. Completely apterous forms are usually, though not always, characterised by great reduction in the tympanal organs, which may become completely obsolete.

The function of tympanal organs has been investigated only quite recently. Indeed, Snodgrass (1935) was very dubious about their auditory function only a few years ago, although by that time Auger and Fessard (1928, 1928a) provided some experimental evidence on this point, by studying the reactions of decapitated *Anacridium aegyptium* to vibratory excitations transmitted by air. Particularly clear responses (movements of legs, wings, etc.) were received to such weak, but high-pitched noises as the rustling of paper, the clinking of glass, etc. This suggested the effects of high frequency vibrations and, by using a series of Koenig's cylinders, reactions were obtained to vibrations of frequencies beyond 20,000 per second, which are not perceptible to the human ear. The auditory function of tympanal organs was proved by the disappearance of response when the organs were destroyed, or smeared with vaseline.

A more exact method was used by Wever (1935) who joined an active electrode to the thoracic ganglion which innervates the tympanal organ, and observed electrical effects produced by sound excitations of definite frequencies. In four individuals of *Arphia sulphurea*, the threshold (lower limit) of sensitivity varied from 300 to 900 cycles per second, and the upper from 18,000 to 21,000 cycles. At low frequencies, the tympanal organ is very insensitive as compared with the human ear. The optimum sensitivity is beyond 10,000 cycles per second, while in man it is at about 1,500 cycles (fig. 8). Wever's data were further supplemented by even more exact experiments of Pumphrey & Rawdon-Smith (1936, 1936a ; Pumphrey 1940) who placed a decapitated *Locusta migratoria* in a sound-proof room and connected the tympanal nerve to an amplifier feeding a cathode ray oscillograph and loud-speaker, so that the nerve reactions could be both seen on a screen and heard. For stimulation, pure and exactly calibrated tones from a beat oscillator and amplifier were used. Since no trace of synchronisation of the response to the stimulus frequency could be observed, the authors were at first inclined to believe that the

locust is unable to discriminate frequency by means of its tympanal organ, but more recently Pumphrey & Rawdon-Smith (1939) propounded a new theory of frequency discrimination. This is based on the experiments in which a locust tympanum was exposed to a sound source yielding pure tones of any frequency up to 10,000 c.p.s. which were modulated



8

Fig. 8.—Threshold curves of the response of the tympanal organ in *Arphia* (A) and in *Locusta* (B), as compared with man (C). Horizontal scale-frequency in cycles per second; vertical—*log.* intensity of sound pressure, i.e. relative loudness of sound. (*After* Pumphrey.)

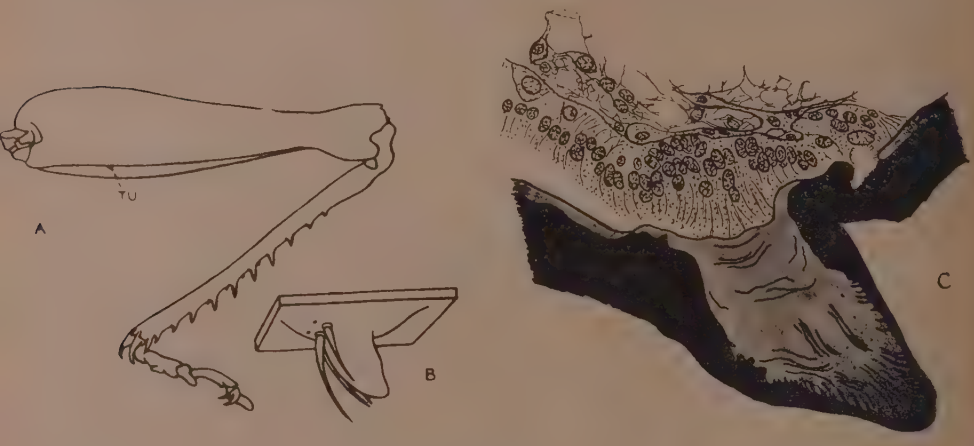
in amplitude at a second chosen frequency. At the pure tone of 8,000 c.p.s., very good response was obtained, but it was completely random. But if the same pure tone was modulated at any frequency up to 300 c.p.s., the response became very characteristic. This suggests that high frequencies have in themselves no significance for the insect, but serve to carry the modulation in the same way as audio-frequency modulation is carried in wireless by high-frequency electromagnetic waves. On the other hand, since the tympanal organs are paired and very sensitive to fluctuations in the intensity of sound (particularly at low absolute intensities), they may be of importance to the locust in locating the source of a sound, such as the stridulation of another locust.

These recent studies make the auditory function of the tympanal organs beyond doubt. In addition a considerable amount of observational evidence on the ability of ACRIDIDAE to hear sound has been accumulated. It is a noteworthy fact, however, that well developed tympanal organs are found even in those ACRIDIDAE which have no sound producing organs.

The tympanal organs are not the only mechanism by which ACRIDIDAE can perceive sounds. Pumphrey & Rawdon-Smith (1936a) have proved, by the same electrical method, that the short-hair sensilla generally distributed over the body of *Locusta* show a nervous response to acoustic stimuli, very similar to the tympanal response, but the range of sensitivity is somewhat different. In a letter to the present writer, Dr. Pumphrey stated, further, that certain sensilla on the cercus of *Locusta* also respond to sounds of low frequency, up to 800 cycles per second. Thus, there are in the locust at least three distinct mechanisms for the reception of sounds and other vibrations.

7. *Brunner's organ.*

In all these ACRIDIDAE there can easily be seen on the underside of the hind femur near its base a small tubercle, which in living insects is soft and flexible. This structure has been recently studied (Slifer & Uvarov 1938 ; Jannone 1939e) and proved to represent a somewhat complicated sense organ (fig. 9). The sensory parts of Brunner's organ are represented by 4–5 long hairs (trichoid sensilla) and a group of



9

Fig. 9.—Brunner's organ in *Melanoplus differentialis*.—A, right leg seen from inside (TU, Brunner's organ) ; B, Brunner's organ with tactile hairs ; C, section through Brunner's organ. (*After* Slifer & Uvarov.)

campaniform sensilla near its base. The interior of the tubercle is filled with a cuticular deposit, while its base rests on a layer of epidermal cells under which there is fatty tissue with a network of nerves. The possible function of Brunner's organ remains enigmatic. In Jannone's (1939e) experiments adults of *Dociostaurus maroccanus* in which Brunner's organ was cut off behaved normally but those in which it was cauterised practically lost their ability to jump. It was possible, however, that in the second lot nerves and muscles were damaged and the suggestion that Brunner's organ is connected with jumping capacity remains

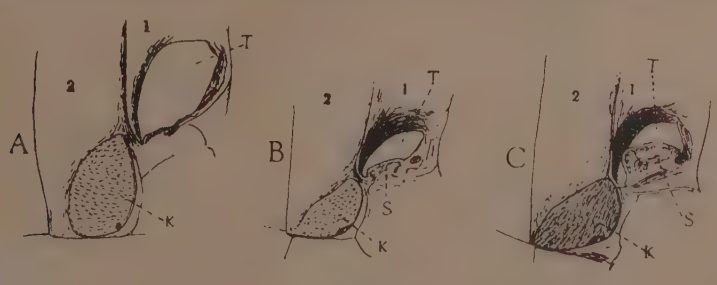
unproved ; it should be noted that other Saltatoria (TETTIGONIIDAE, GRYLLIDAE) are able to jump although they have no Brunner's organ. Another suggestion would be that Brunner's organ has something to do with the normal resting posture of a grasshopper, when the tibia is pressed closely to the femur, thus flattening the tubercle, but there is no experimental evidence of any kind in support of this view. No correlation has been found between the degree of development of Brunner's organ and the ecology of various ACRIDIDAE and the whole problem remains open for investigation.

8. *Prosternal tubercle.*

According to Chauvin (1939b, 1941c), the prosternal tubercle of *Schistocerca gregaria* is covered by a thick cuticle bearing sensory hairs ; under the cuticle lie pigmented hypodermal cells ; and the central cavity is filled by the adipose tissue and by large tracheae. There is no direct evidence on the function of the tubercle, but its development appears to be connected with climbing habit, and it may be suggested that it represents a tactile organ enabling an Acridid to maintain close contact with the plant when climbing.

9. *Krauss' organ.*

In most members of the subfamily PAMPHAGINAE, an oval plate, covered with tubercles, or ridges, can be seen on the lower anterior



10

Fig. 10.—Krauss' organ in *Prionotropis hystrix* (A), *Asiotmethis muricatus* (B) and *Tmethis cisti* (C).—1, first tergite ; 2, second tergite ; K, Krauss' organ ; T. tympanum ; S, subtympanal lobe. (*After* Uvarov 1943.)

corner of the second abdominal tergite (fig. 10). The plate was formerly supposed to be a sound-producing organ but its structure is against this view (Uvarov 1943) and the problem awaits a thorough study.

10. *Various sensilla.*

Very detailed anatomical and histological descriptions of different types of sensilla in *Dociostaurus maroccanus* have been presented by

Jannone (1939e). About 33–35 *campaniform* sensilla are placed in 1–3 series around the distal end of the second antennal joint, and others of similar type occur in groups on the trochanters and femora of the first and second legs ; somewhat modified campaniform sensilla are found on the pulvilli of the first tarsus. Sensilla of the *coeloconic* type are found on the antennae, their total number in a first stage hopper being 125 and in an adult female, 470–490 ; in the latter, none are found on the first three joints and the number on each of the following joints varies from 4–53. *Basiconic* sensilla are also found on the antennae, but in greater number than the coeloconic. *Trichoid* sensilla, or sensitive hairs are found on various parts of body, but particularly on the antennae, mouth parts, etc. Specialised hair sensilla on the cerci have a complicated basal mechanism ; Jannone considered these sensilla as tactile, but it is more probable that they are the acoustic sensilla of Pumphrey (p. 30).

Practically nothing is known on the function of the various sensilla, except that the campaniform ones, formerly regarded as " olfactory pores " (McIndoo ; *see* Uvarov 1928a) have been found, in the cockroach, to give no electrical response to chemical excitation. On the other hand, definite proofs were obtained that the campaniform sensillum is a mechanical receptor responding to stresses in the cuticle ; certain hair sensilla on the legs of cockroach also proved to respond to mechanical excitation (Pringle 1938, *J. exper. Biol.* **15**: 101–131 ; 467–473).

The scarcity of knowledge on the structure and function of sensilla in ACRIDIDAE is deplorable, since apart from their importance in behaviour, sensilla should play an important part in the sensitivity of these insects to contact insecticides.

XIV. SOUND-PRODUCING ORGANS.

The number of known types of sound-producing mechanisms known in ACRIDIDAE (Uvarov 1929) has somewhat increased, although no comprehensive investigations of the problem have been made. Henry (1940, *Trans. R. ent. Soc. Lond.* **90** : 513) has presented a detailed illustrated description of the mechanism in *Psectrocnemus* where the posterior tibial spines are expanded and finely ridged, to act as scrapers against the raised radial vein of the elytron which is strongly tympanate. The same author (Henry 1942) has described three other quite different types. In *Charora*, the tergites 4–8 of the abdomen bear 10–20 strongly raised parallel ridges running vertically ; spines of hind tibia are laterally compressed and have sharp edges ; a rasping sound is produced by scraping the spines against abdominal ridges, but direct observations on the action of the mechanism in the live insect are lacking. In the remarkable *Phonogaster cariniventris*, the hind femur has the usual stridulatory pegs, but the elytra are not modified for stridulation, and, instead, the sides of the abdomen are provided with two raised ridges running horizontally on the segments 3–5, which have very thin translucent walls and are almost entirely filled with large air-sacs, acting as resonaters. In *Mesambria* a shrill creaking sound is produced by movements of

mandibles, while *Oedaleonotus* produces a clicking sound by the same means (Varley 1939).

A cursory examination of a representative collection of ACRIDIDAE shows that several more types of stridulatory mechanisms can be brought to light by careful studies. On the other hand, the abdominal mechanism described for *Tmethis* (Uvarov 1928a) is now suggested to be unsuitable for sound-production and to represent a sense organ (p. 31).

Since stridulation is connected with various activities, it is more convenient to discuss it in the summary on behaviour.

XV. REPRODUCTIVE SYSTEM.

1. *Male internal organs.*

Recent descriptions of the whole of the male reproductive system are available only for *Dociostaurus maroccanus* (Jannone 1939e) and *Chorthophaga viridifasciata* (M. A. Payne 1933), and comparative studies of a large number of species are still to be made. Such a study undertaken by Laird (1943), although referring only to the gross morphology of the testes proper, has shown a considerable variety of structure. The testes of about a hundred species studied can be referred to three types (fig. 11).

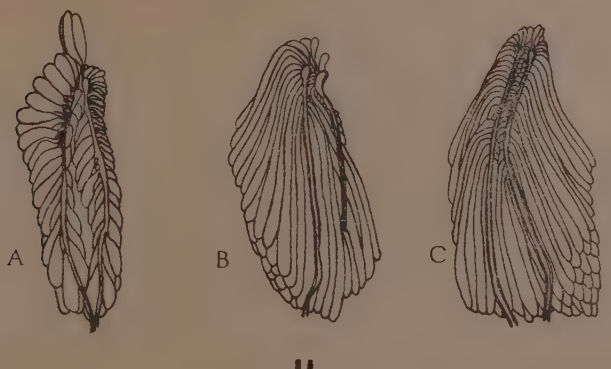


Fig. 11.—Testes of three different types. —A, radiating, *Sphenarium mexicanum*; B, fountain, *Xanthippus corallipes*; C, intermediate, *Melanoplus mancus*. (*After* Laird 1943.)

The simplest type is the radiating (A), in which the paired follicles enter the seminal ducts (vasa efferentia) along the whole length of the testis and radiate from it as an axis. In the fountain type (B), the follicles tend to enter the duct near its blind end in a cluster. The difference between the two extreme types is considerable but they are connected by transitional forms; these are referred to an intermediate type (C),

in which the follicles enter the ducts for a distance of about one half of the whole testes. The author believed to have established some correlation of the testis type with the subfamily position of each genus, but this claim is scarcely justified, since variations from the intermediate to the fountain type occur in the genus *Schistocerca*, and in *S. americana* even all three types are found. Laird's studies on the postembryonic development of the testis have shown that all types develop from the radiating one, so that the difference between them is merely one of degree of follicular clustering which has no phylogenetic meaning. Another study of testes has been made by Chen (1933), on five Chinese species, including *Locusta migratoria*; his statement that the testis in *Acrida turrita* is unpaired appears very doubtful.

The number of follicles in a testis is subject to some individual variation and to a more significant one between species (Laird *l.c.*; Chen *l.c.*; Nolte 1939). According to Laird, the number is usually very great in the testes of the radiating type, e.g. 250 in *Romalea microptera*, while in the intermediate testis the number is less, 100–150, and in the fountain one quite small, 14–100; thus, the clustering of follicles goes with a reduction in their number, but individual follicles become much more elongated and slender.

Some histological data on the walls of the seminal vesicle and the accessory glands in *Schistocerca gregaria* have been published by Chauvin (1941c), while Roonwal (1935) recorded an abnormal structure in the accessory gland of the same species.

2. *Female internal organs.*

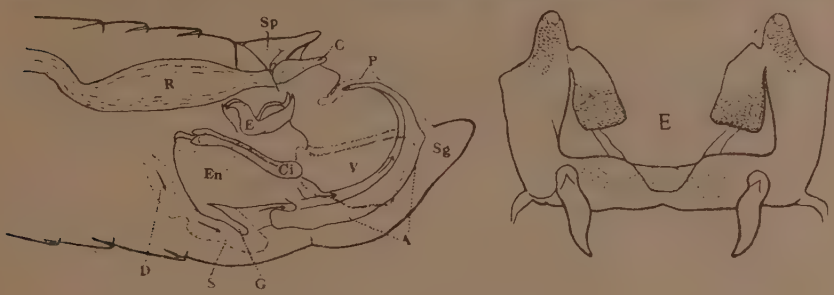
A general description of the internal reproductive organs in a female was presented for *Locustana pardalina* by Nel (1929). He has also studied these organs in *Colemania sphenarioides*, a Pyrgomorphine, but gave no description, remarking merely that their general plan was the same as in *Locustana*. Accounts of the female genital ducts by Heberdey (1931; cf. criticism by Slifer 1939) and Qadri (1940) are diagrammatic.

Partial work on reproductive organs mostly concerns the ovarioles (egg-tubes). According to Nelsen (1934) who gave a histological description of an ovariole and of the gonadal portion of the oviduct, the ovariole is an elongated tube which can be divided into three zones. The first zone, nearest the oviduct, contains growing eggs in various stages; the second contains oogonia; the third is a very narrow terminal filament. There are considerable differences in the number of ovarioles in different species, as well as in individuals of the same species (Rubtzov 1934; Nolte 1939). Since their number has a direct bearing on the fertility, the relevant data will be reviewed elsewhere.

3. *Male genitalia.*

Excellent treatment of the male copulatory apparatus will be found in Snodgrass' papers (1935, 1936, 1937), where a general discussion of its various parts, including the musculature, is followed by a series of examples of the variations observed in different genera.

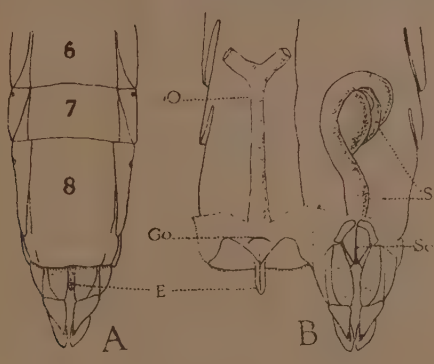
Descriptions of the male genitalia have also been given by Boldyrev (1929 ; *Locusta migratoria ;* an excellent treatment in which all structures are discussed with reference to their function in copulation ; see fig. 12) ; Else (1934 ; *Melanoplus differentialis*) ; Guarino (1935 ;



12

Fig. 12.—Male genitalia of *Locusta migratoria*.—R, rectum ; Sp, supraanal plate (epiproct) ; C, cercus ; P, pallium ; E, epiphallus (enlarged on the right) ; En, endophallic plates ; Ci, cingulum ; V, ventral valve ; Sg, subgenital plate ; A, aedeagus (penis) ; D, ejaculatory duct ; S, ejaculatory sac ; G, gonopore process. (*After* Boldyrev 1929).

Anacridium aegyptium including discussion of musculature) ; and Qadri (1940, *Locusta migratoria ;* diagrammatic). The use of genital armature for taxonomic purposes is on the increase, and Roberts (1941) has presented a comparative study of the male genitalia in the various groups



13

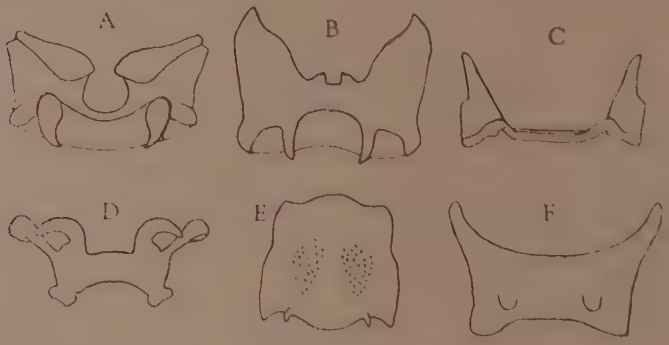
Fig. 13.—Female genitalia of *Locusta migratoria*.—A, ventral view ; **B, do.,** but cut open. O, oviduct ; Go, genital opening ; S, spermatheca ; So, **spermathecal** opening ; E, egg-guide. (*After* Boldyrev 1929.)

of ACRIDIDAE. His re-classification of subfamilies on the basis of male genital structures alone has been criticised (Uvarov 1943), but his

work should supply a stimulus for further investigations. An excellent example of the great diversity in male genitalia is offered by the epiphallus (fig. 14).

4. *Female genitalia.*

Snodgrass (1935) has provided a description and discussion of the female genitalia in ACRIDIDAE generally ; those of *Locusta migratoria* have been described by Boldyrev (1929 ; see fig. 13) and Qadri (1940) ;



14

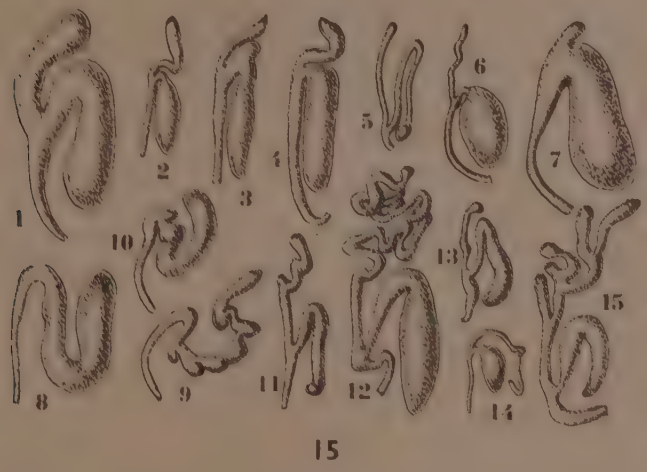
Fig. 14. Epiphallus in various ACRIDIDAE. A, *Oedipoda coerulescens* ; B, *Melanoplus femur-rubrum* ; C, *Chromacris colorata* ; D, *Chrotogonus trachypterus* ; E, *Euryparyphes flexuosus* ; F, *Calliptamus italicus*. (*After* Roberts 1941, modified.)

of *Anacridium aegyptium* by Guarino (1935) ; of *Locustana pardalina* and *Colemania sphenarioides* by Nel (1929) ; of *Arphia xanthoptstera* and other grasshoppers by Slifer (1939).

The anatomy and histology of the spermatheca have been described by Paoli (1937) in *Dociostaurus maroccanus*, and Slifer's (1939, 1940, 1940a, 1940b, 1943) survey of the types of spermatheca in different groups and subfamilies of ACRIDIDAE has shown a great variation (fig. 15) that promises to be of considerable taxonomic value.

Another interesting feature of the female genitalia is provided by the paired glandular pouches lying on both sides of the vagina, each with its own opening. These pouches were first described by Comstock & Kellog (1899, *The elements of insect anatomy*) and then again by Vardé (1929, 1934) who has called them "oviductal vesicles." In view of their glandular nature, it appears appropriate to call them the *Comstock-Kellog glands*. Slifer & King (1936) and Slifer (1939, 1940a) have found these glands in practically all the members of the subfamily CATANTOPINAE, but not in ACRIDINAE, OEDIPODINAE and PYRGOMORPHINAE. The glands are found without difficulty on dissection because they are

usually pigmented (red, brown, orange, etc.). Their function is not known. Vardé (*l.c.*) noted that they are eversible and suggested that they may be odoriferous and play a part in the attraction of the male by the female



15

Fig. 15.- Spermatheca in various ACRIDIDAE.—Subfam. ACRIDINAE: 1, *Acrida turrita*; 2, *Gomphocerus sibiricus*; 3, *Aulocara elliotti*; 4, *Chorthippus longicornis*; 5, *Orphulella concinnula*; 6, *Stauroderus scalaris*. Subfam. OEDIPODINAE: 7, *Arphia xanthoptera*. Subfam. PAMPHAGINAE: 8, *Oeneridia sp.* 9, *Tmethis cisti*. Subfam. PYRGOMORPHINAE: 10, *Poecilocerus vittatus*. Subfam. CATANTOPINAE: 11, *Hieroglyphus annulicornis*; 12, *Anacridium aegyptium*; 13, *Melanoplus femur-rubrum*; 14, *Paraidemona mimica*; 15, *Teratodes monticollis*. (*After* Slifer.)

at the time of copulation. Hubbell & Cantrall (1938) have actually observed the glands in everted state before copulation in *Appalachia arcana*.

5. *Gynandromorphism.*

Several cases of gynandromorphic individuals have now been described in the following species: *Oedaleonotus phrynicicus* (Hebard 1919, *Trans. Amer. ent. Soc.* **45**: 268, footnote); *Podisma sapporensis* (Natori 1931; including the cytology); *Melanoplus adelogyrus* (Hubbell 1932, *Michigan Mus. Zool., Misc. Publ.* **23**: 39); hybrid between *Trimerotropis citrina* and *T. maritima* (Carothers 1939); *Anacridium moestum* (Potter 1940); and *Camnula pellucida* (Paul 1941). In most of the cases, the gynandromorphism was incomplete and restricted to the external parts. Severin (1943) has reported a specimen of *Melanoplus mexicanus* which was typically male on both sides dorsally and typically female in the ventral right half of the body; but this case was not studied anatomically.

XVI. METABOLISM.

We have already reviewed the meagre data referring to the nutritional metabolism (p. 13). The present section contains information on the chemical constitution of ACRIDIDAE, on their gaseous metabolism, and their water and heat balance. Metabolic processes connected with the oogenesis and those occurring in the developing egg will be reviewed in the summary dealing with the development.

1. *Chemical composition.*

Complete quantitative analyses of the mineral ash content exist only for two species of ACRIDIDAE, *Schistocerca gregaria*, sexually mature adults (E. B. Uvarov 1931) and *Oxya velox* (Takata & Korigawa 1934; Ichikawa 1936, 1936a, 1937; Itikawa 1940). The results are combined in Table VIII.

TABLE VIII.

Ash analyses of *Schistocerca gregaria* (after E. B. Uvarov) and *Oxya velox* (after Ichikawa).

	Schistocerca gregaria	*Oxya velox*	
		Males	Females
SiO_2	11·9	6·638	9·611
CuO	0·16*	—	—
Fe_2O_3	2·06	1·593	0·687
MnO	0·21*	0·255	0·306
Na_2O	6·2	17·102	20·208
K_2O	18·2	21·776	19·230
CaO	6·2	1·053	0·735
MgO	4·9	5·437	3·852
TiO_2	0·16	—	—
NiO	0·009	—	—
P_2O_5	32·4	40·095	46·263
SO_3	2·56	0·671	0·272
Cl	0·40	—	—
C	2·4	—	—

* Re-calculated from the original figures which are for Cu and Mn.

When the two species are compared, it appears that *Schistocerca gregaria* is distinguished by its considerably higher calcium and sulphur and iron content, but it is poorer in sodium and phosphorus than *Oxya velox*. Differences in other figures are less conspicuous and may have no significance.

Differences between the sexes of *Oxya velox* are not great, except in the case of magnesium and phosphorus, the first showing higher content in the male, and the second in the female; these differences may be due

to different composition of mature gonads. The ash of *Schistocerca gregaria*, according to Lapp & Rohmer (1937) contains in addition to the elements enumerated in Table VIII, also lithium, barium and strontium, but these authors analysed locusts sold in a Moroccan market, boiled in salt water. Moxon (1939) found a high selenium content, ranging from 3·9 to 20·9 per cent. in *Melanoplus bivittatus* but this may have been due to the stomach contents, as the insects were feeding on seleniferous plants in South Dakota. In *Taeniopoda auricornis* and *Melanoplus sp.* sulphur was found in fats (F. Giral 1941 ; J., F. & M. Giral 1943, 1944).

A partial colorimetric analysis of *Acanthacris ruficornis* showed a relatively high (0·43 per cent. of total ash) copper content (E. B. Uvarov 1931). In adults of *Melanoplus femur-rubrum*, Melvin (1931) reported 69·3 mg. of copper per kg. of dry weight, but the copper content was higher in the cast off skins (presumably of last stage hoppers) than in the whole insect. Colorimetric analyses of the sexually immature (red coloured) and the sexually mature (yellow) *Schistocerca gregaria* proved a considerable reduction in the silica content with maturation (E. B. Uvarov, 1931).

Quantitative studies on manganese in insects, including a number of ACRIDIDAE, were made by Vinogradov & Neustrueva (1930 ; Vinogradov 1937). The percentage of that element in relation to the total live weight varied from 0·0011 to 0·0031, the range of specific differences being relatively small. Some differences were observed between the sexes ; thus in the males of *Locusta migratoria* ph. *solitaria* the manganese content was found to be 0·0021, while in the females it was 0·0014, but the significance of this difference is not clear.

Kunasheva (1932) found that the carbon content in five species of ACRIDIDAE varied from 14·9 to 16·92 per cent. of live weight. Determinations in different stages showed that the carbon content gradually increases during hopper development. Adult females, as a rule, have a higher carbon content than males (see also Vinogradov 1929).

2. *Proteins.*

As regards organic constituents, Korigawa (1934) gave the following table (Table IX) for *Oxya* spp., which shows a very high protein content.

TABLE IX.

Organic constituents of *Oxya* spp. (after Korigawa).

Moisture	11·08—12·48
Total N.	10·79—10·90
Crude protein	67·44—68·13
Protein N.	7·36— 7·54
Protein	46·00—47·22
Amino N.	0·76— 0·80
Crude fats...	4·42— 4·61
Crude ash	3·67— 3·88
Chitin	9·13— 9·36
Glycogen	0·01

Similar results were obtained with the last stage hoppers of *Nomadacris septemfasciata*, which proved to contain 46·1 per cent. of protein and 9·6 per cent. of fat. This makes locust meal very suitable for use in stock feeding as a substitute for oil-cake (Adler *et al.* 1934). In *Schistocerca gregaria* the protein content was found to be 56·7 per cent. in the case of males, and 42·3 per cent. in females (Lapp & Rohmer 1937). Das (1945) estimated, in the same species, 61·75 per cent. protein and 18·95 per cent. fat.

Analyses of proteins were given for *Oxya* spp. by Korigawa (1934, 1934a) and Ichikawa (1938); see Table X.

TABLE X.

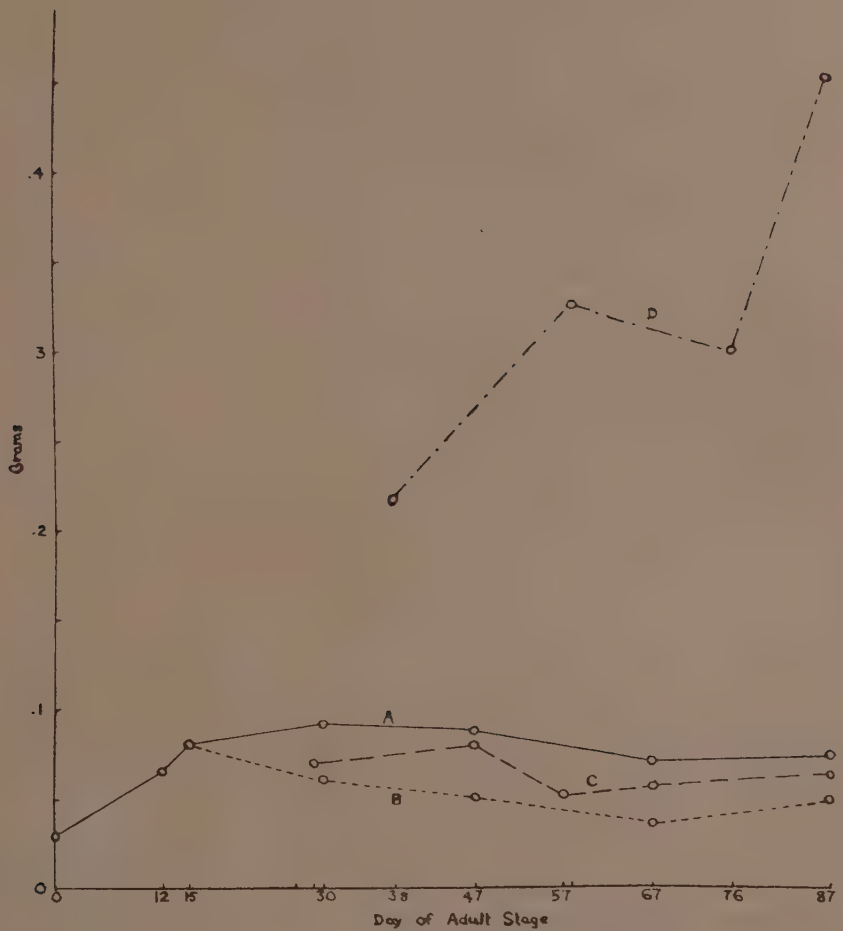
Protein analysis of *Oxya velox* (after Ichikawa).

	Males	Females
Water soluble N	36·49	35·00
Albumine N	6·68	10·22
Globuline N	8·51	7·10
Prolamine N	1·51	1·84
Gluteine N	21·84	21·81
Chitin N	25·00	24·03

3. *Fats.*

The data on total fat content in *Nomadacris* and *Schistocerca* quoted above are too general to be of value in studies on fat metabolism, and the only source of information on the latter subject is a paper by Weed Pfeiffer (1945a). According to that author the fat body in newly moulted adult females of *Melanoplus differentialis* was small, by the fifteenth day it increased considerably, but then a reduction commenced and the condition of the fat body approached the initial one (fig. 16). This suggests that the fat body at first is synthesized and stored, but later it is expended at a greater rate than synthesized ; this expenditure is connected with egg development and will be discussed in the appropriate summary. The ratio of fatty acids to dry weight varies from 14 per cent. on the day of moulting to 15·6 per cent. on the 12th day and to 10·8 per cent. on the 67th day of adult life ; these percentages, however, do not represent a true picture, since the dry matter content is also subject to metabolic changes. The role of corpora allata in fat metabolism is strikingly illustrated by curve D in fig. 16.

Timon-David (1930) presented an excellent summary of data, both from the literature and from personal investigations, on fats and oils of insects, including some ACRIDIDAE. Table XI summarises the essential characteristics of Acridid fats as given by various authors (see also F. Giral, 1946 ; J. F. & M. Giral, 1946).



16

Fig. 16.—Fatty acid content in adult females of *Melanoplus differentialis*. —A, normal females; C, castrated females; D, females with corpora allata removed; B, weight of fatty acids estimated to be located elsewhere than in the eggs. (*After* Weed Pfeiffer 1945a.)

TABLE XI.

Characteristics of fats extracted from ACRIDIDAE.

Species	% Wet body weight	Iodine index	Saponification index	Reference
Dociostaurus maroccanus ...	3·3	109·9	181·0	Timon-David 1930
Anacridium aegyptium ...	2·57	97·6	198·9	Do.
Schistocerca gregaria, ♂ ...	—	106·68	224·0	Lapp & Rohmer 1937
Schistocerca gregaria, ♀ ...	—	92·71	224·0	Do.
Schistocerca paranensis ...	—	65·2	194·5	Trewithick & Lewis 1939
Oxya japonica	3·00	122·6	171·5	Tsujimoto 1929
Taeniopoda auricornis, ♂	2·52	111·5	196·5	F. Giral 1941
Taeniopoda auricornis, ♀	2·76	101·3	185·0	Do.
Melanoplus mexicanus ...	—	75·3	216·3	J. F. & M. Giral 1943

Those fats which have been studied in greater detail, proved to contain linolenic, linoleic and oleic acids. The fat of *Taeniopoda* contains 0·247 per cent. sulphur in the females and 0·096 per cent. in males; it causes fatal effects when injected into rats and frogs, while the proportion of sulphur in the fat of *Melanoplus* is only 0·032 per cent. (F. Giral 1941, J., F.&M. Giral, 1944). All these data on fats are obviously quite preliminary and further studies are required on fats and their metabolism in different species, and stages of development. Recent work by Matthée (1945) indicated considerably higher fat content in the gregarious phase of *Locusta migratoria* and *Locustana pardalina* than in the solitary.

4. *Chitin.*

Rotman (1929) has done some work on the estimation of the percentage of total chitin in *Locusta migratoria* in relation to dry body weight; and Millot and Fontaine (1938) estimated its percentage to total body weight in *Schistocerca gregaria*. The results of these two investigations are presented in the Table XII, where by chitin is meant the total residue insoluble in KOH, although not all of it is necessarily chitin in the chemical sense.

TABLE XII.

Chitin content of locusts.

Stages	*Locusta* % of chitin to dry weight	*Schistocerca* % of chitin to wet weight
Hopper, 1st stage	4·72	—
,, 2nd ,, ...	6·53	—
,, 3rd ,, ...	7·31	2
,, 4th ,, ...	6·93	1·7
,, 5th ,, ...	9·22	2·2
Adult, age unknown	10·20	—
,, newly moulted	—	1·3
,, 2 days old	—	2·2
,, 7 ,, ...	—	3·2
,, 2 months old	—	4

In the case of adult *Locusta*, the percentage of chitin to wet weight would be 3·39 per cent., a figure very close to that given by the other two authors for old adult *Schistocerca*. The figures suggest that the total chitin content in ACRIDIDAE is low as compared with other insects, since in beetles, for instance, it fluctuates between 5 and 15 per cent. It is of interest to note, further, that the differences in the chitin content between developmental stages are small and perhaps not significant. On the other hand, the figures for *Schistocerca* indicate a strong increase in chitin content with the ageing of the adult, obviously in connection with the thickening of the cuticle (p. 6).

It would be of interest to study the distribution of chitin in different parts of the body. Another problem worthy of attention is the quantitative determination of chitin content in ACRIDIDAE from different habitats. Even superficial observation shows for example that the integument of desert species is much thicker and harder than of those living in mesophilous grass habitats.

5. *Vitamins.*

High vitamin content in *Oxya* sp. (Inafu 1936 ; Takata & Korigawa 1934), and considerable quantities of vitamin A and of vitamin B_1 in *Melanoplus differentialis* (Macht 1937) have been reported, but details are not available. J., F. & M. Giral (1944) found no trace of vitamin A in *Taeniopoda auricornis*. Flavin and riboflavin (vitamin B_2) were found in the Malpighian tubes of *Schistocerca gregaria* (Gourevich 1937 ; Drilhon & Busnel 1939 ; Busnel & Drilhon 1942 ; Drilhon 1943).

6. *Pigments.*

The morphological aspects of Acridid colouration have already been mentioned (p. 7) and its ecological significance will be discussed in the corresponding summary. Pigments, however, do not exist in the organism merely to produce its visible colouration, but they play their part in metabolic processes, though so far this part is largely obscure.

The black and dark patterns of ACRIDIDAE are due to deposits of melanin which are mainly concentrated in the cuticle, as can be seen in the exuviae of hoppers which present the typical black pattern (Chauvin 1939b). The distribution of melanin in the cuticle in many cases appears to bear relation to the intensity of local metabolism in the tissues immediately below, since dark patches often occur, for example, over the insertion of muscles (Wigglesworth 1939). Black spots and stripes are common components of pattern of both hoppers and adults and Chauvin's (1939b, 1941c) statement that there is no melanin in the integument of adult *Schistocerca gregaria* appears puzzling, since in that species there are, at least, blackish spots on the elytra which are probably formed by melanin. In *Mesopsis*, melanin formation occurs actually during adult life when it is deposited in the wings (Burtt & Uvarov 1944). Broussy (1933) described pigment granules in hypodermal cells of *Anacridium aegyptium* which he believed to be chemically close to melanin, but Chauvin regarded apparently analogous pigment inclusions in hypodermal cells of *Schistocerca gregaria* not as melanin,

but as a pigment of anthocyanin group which he called acridioxanthin (*see* below). The melanin of *Schistocerca*, according to Chauvin (1941c) is produced by dopa-oxidation and not by tyrosinase, but the difference between the two seems to be a quantitative one and in either case tyrosinase is the enzyme concerned (Wigglesworth 1939). Chauvin (1941c) reported melanin not only in the cuticle but also in pericardial cells and in those of the salivary glands of *Schistocerca*.

Carotenoid pigments, or lipochromes, are mainly responsible for yellow colours. The well-known bright yellow colouration of sexually mature *Schistocerca gregaria* is due to a carotenoid pigment deposited at the limit between hypoderm and cuticle. Sexually immature *Schistocerca* owes its pink colour to a xanthophyll (dioxide of carotin), found in solution in the fat globules of hypodermal cells (Chauvin 1941c). Carotenoid pigments were found also in the oenocytes of *Schistocerca* (Chauvin 1937, 1938d, 1939a, 1941c). In *Melanoplus bivittatus*, yellow pigment was identified as a carotin with traces of a xanthophyll ; it was found mainly in the body cavity, and its concentration averaged 0·0397 mg. per gram of body weight in the males, and 0·0436 mg. in females, but in the reproductive organs and the surrounding fatty tissues the concentration rose to 0·266 mg. per gram (Grayson 1942 ; Grayson & Tauber 1943). It is possible that the orange-red pigment found by Roonwal (1945a) at the base of ovarioles of *Schistocerca gregaria* was also a carotenoid ; it certainly was not identical with the acridioxanthin of Chauvin (*see* below) as Roonwal suggested. Lederer (1934, 1938) and Okay (1945) reported carotenoid pigments in red-coloured hind wings of *Oedipoda germanica* and the latter author gave it the name of *orthopteroerythrin*. Chauvin's (1939) experiments in rearing *Schistocerca gregaria* on food devoid of carotins proved that carotenoid pigments are derived from carotin in food.

In a series of papers, Chauvin (1938c, 1938d, 1938e, 1939, 1939d, 1940, 1941b, 1941c, 1944) dealt with a pigment found in the form of brownish grains in hypodermal cells of *Schistocerca gregaria* ph. *gregaria*. At first, he identified it with a melanin, but later referred it to *anthocyanins*. According to Chauvin, this hypodermal pigment is responsible for the brownish colouration of the immature adult, and for its reddening when put into boiling water. Similar reddening is caused by alcohol, by benzene and by decomposition in water as well as by reducing substances, such as sodium hydrosulphide ; the original colour can be restored by the action of oxygenated water and the process can be repeated several times. The pigment is soluble in cold absolute alcohol with 5 per cent. hydrochloric acid, and in very weak alkalis ; the alkaline solutions are yellow, but become red if acidified. The yellow pigment has been called by Chauvin *acridioxanthin*, and its red derivative *acridioerythrin*. It is derived from food and its quantity increases during the hopper stages, but in the young adult practically all of it is eliminated with the excreta which are at that period coloured pink by acridioerythrin. Acridioxanthin was found in several other ACRIDIDAE (*Stenobothrus* sp., *Acrida* sp., *Locusta migratoria*, *Oedipoda miniata*, *Anacridium aegyptium*) but it was absent in the solitary phase of *Schistocerca gregaria*. In fact,

Chauvin considered acridioxanthin as the main basis of biochemical difference between the two phases in that species, but further studies on the nature and properties of Chauvin's pigment must be awaited before such deductions can be made. Grayson & Tauber (1943) found no anthocyanin in *Melanoplus bivittatus*.

The green colouration which is so frequent amongst ACRIDIDAE is due to a pigment diffused in cuticle, but its nature remains uncertain. Since in Faure's (1932) experiments hoppers of various locust species tended to become green on fresh green food, it was natural to suggest that the colouration is due to chlorophyll, but neither chemical nor spectroscopic tests of extracts from green hoppers have shown its presence. Experiments with feeding hoppers on plants devoid of chlorophyll were inconclusive. In Chauvin's (1939a) similar experiments with *Schistocerca gregaria*, hoppers developed a faint greenish tinge in the fifth stage, in spite of a complete absence of chlorophyll from the diet. This author suggests that this may be due either to a relic of chlorophyll from the egg or to a pigment synthesized by hoppers. In his latest paper Chauvin (1941c) suggests that the green pigment of solitary hoppers may be a *flavone*.

Przibram & Lederer (1933, *Anz. Akad. Wiss. Wien* **70** : 163–165) suggested that the green colour of Phasmids and Mantids is due to a mixture of a yellow carotenoid pigment and of a blue water-soluble one. Okay (1945) made the same suggestion with regard to *Acrida turrita*, and he gave the name *orthopterocyane* to the yellow pigment and *orthopterocyanobiline* to the blue.

Pigments of the flavin group were recently reported in *Schistocerca gregaria* (Gourevitch 1937 ; Drilhon & Busnel 1939 ; Busnel & Drilhon 1942 ; Drilhon 1943). Riboflavin was found in the tissue of the Malpighian tubes, but it was not excreted ; it also was found in eggs where its content increased with the development. Other fluorescent pigments found in the Malpighian tubes included lumiflavin, lumichrome and two substances with blue fluorescence (Busnel & Drilhon 1942). The same authors reported the presence in *Schistocerca gregaria* of a pigment of the pterine group.

The factors of pigment metabolism remain unstudied. Olsen's (1943) experiments with the effects of coloured lights on the deposition of pigments in two species of ACRIDIDAE have not yet been described in full, but they do not appear to go beyond purely empirical deductions ; the same is largely true for experiments by Hertz & Imms (1937) on effects of coloured lights on the colouration of *Locusta migratoria*. Extracts from heads of some ACRIDIDAE proved to cause contractions of chromatophores in Crustaceans, as Hanström (1936–1940a) has shown and he suggested that an organ in the head (possibly corpora allata) produces a hormone affecting pigment metabolism.

It will be seen that the available information on Acridid pigments and their metabolism is too scanty and disjointed to be of general value. On the other hand, it would appear that a thorough study of pigment metabolism may be of considerable assistance in the understanding of a number of aspects in Acridid biology, e.g. phase transformation,

colour adaptation to background, thermal economy, etc. There is a fertile and almost virgin field for research, but it is to be hoped that such research will be undertaken by highly trained biochemists in well equipped laboratories. Attempts made by entomologists at identifying pigments by a few simple reactions, followed by giving them long but meaningless names, should be discouraged as they are likely to introduce more confusion than clarity.

7. *Gaseous metabolism.*

Quantitative studies on the respiratory metabolism in ACRIDIDAE at rest were recently carried out by a number of authors working with different species (*Melanoplus differentialis*, Rogers 1929; Hiestand 1932; Riehl 1943; *Chorthophaga viridifasciata*, Kleinman 1934; same species and *Dissosteira carolina* McGovran 1931; *Gastrimargus transversus*, Koidzumi 1934–5; *Schistocerca gregaria*, Bodenheimer 1929a; *Locusta migratoria*, Butler & Innes 1936). The chief result of these studies was to confirm earlier data (Uvarov 1928a) with regard to the influence of temperature on the rate of gaseous metabolism.

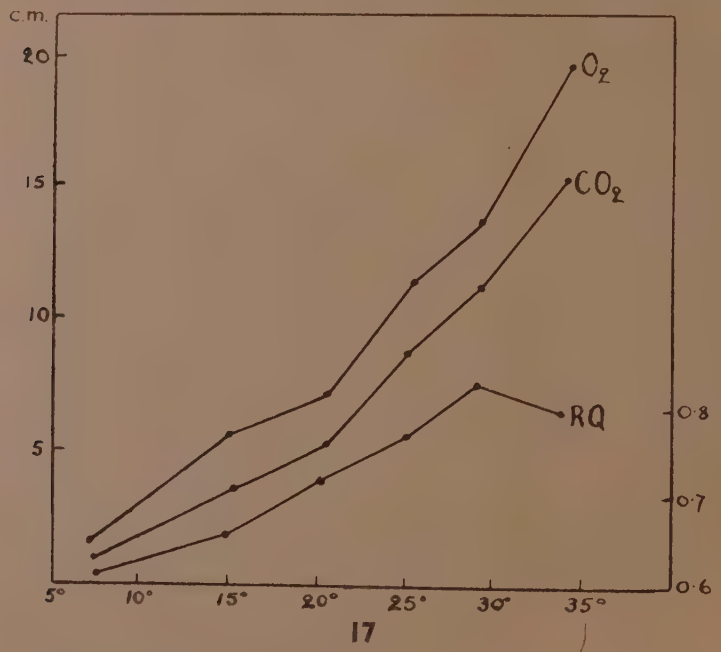


Fig. 17.—Effects of temperature on oxygen consumption (O_2), on carbon dioxide production (CO_2) and on the respiratory quotient (RQ). (*After* Kleinman 1943, modified.)

Both the oxygen consumption and the carbon dioxide output increase strongly with rising temperature. The respiratory quotient (the ratio between CO_2 output and O_2 consumption) also increases with the

temperature, (fig. 17). The mathematical relations between the increase in respiratory metabolism and temperature remain insufficiently clear and the views of various authors differ. Thus, Rogers believed that his data agreed with the formula of Arrhenius, but not of Krogh ; Koidzumi supported van't Hoff's rule ; Bodenheimer interpreted his results as agreeing best with Krogh's logarithmic curve ; and Kleinman stated that the relations between the rate of respiration and temperature could not be correctly expressed by any of the above formulae. A discussion of the formulae and curves by Wigglesworth (1939) leads to the conclusion that " they have some descriptive value but none of them is of sufficiently general application to be regarded as embodying any rational principle."

The absolute quantitative data on oxygen consumption and its variation with temperature and with the postembryonic development can be seen in Table XIII.

TABLE XIII.

Oxygen consumption of *Schistocerca gregaria* in different stages and at different temperatures, calculated in c.c. per 10 g. body weight in an hour (after Bodenheimer 1929a).

Temp. °C.	Eggs	Hoppers			Adults		
		1st stage	3rd stage	5th stage	Young ♂	Young ♀	Old ♀
14—15	0·68	2·21	1·83	0·63	2·40	1·87	0·65
19—20	0·73	4·36	3·17	1·44	2·63	1·88	0·81
24—25	0·86	4·87	3·92	2·01	6·97	3·80	1·82
29—30	0·95	4·84	5·58	4·34	10·86	4·98	3·15
34—35	1·14	6·70	6·75	5·06	13·72	6·80	4·73
39—40	1·32	8·62	10·38	6·26	8·91	8·90	8·73
43—44	2·82	9·48	12·50	5·79	7·22	7·29	8·59

The table shows that the amount of oxygen consumed per unit of body weight decreases as the hopper grows. This progressive diminution of the rate of metabolic exchange with the growth of the insect suggests the applicability of Rübner's law, according to which the intensity of gaseous metabolism in a growing animal increases in proportion to the increase in its surface area, and therefore becomes progressively smaller per unit of weight. Butler & Innes (1936) have studied the metabolism in *Locusta migratoria* in various stages, calculating the amount of oxygen consumed in relation to a unit of surface area and obtained a confirmation of Rübner's law. Riehl (1943), however, working with all stages of *Melanoplus differentialis*, found that the rate of oxygen uptake agreed with Rübner's law only at 80° F., while in the fourth instar hoppers at 65°, 70°, and 80° F., it was higher than required by the law, and at 40° F. the rates did not differ significantly between all instars.

Both Bodenheimer and Butler & Innes observed a distinct difference in the rate of oxygen consumption at the same temperatures between the two sexes of adult locusts. As can be seen from Table XIII at temperatures of about 30–35° C. the rate of respiration in males is nearly twice as high as in females. A marked reduction in the respiratory rate in old females, as compared with the recently moulted ones, can also be seen from the table. In *Melanoplus differentialis*, females have a higher oxygen uptake than males during the first two weeks of adult life, but

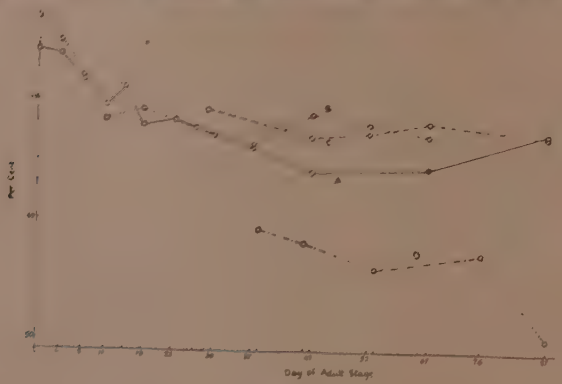
females show a significant decrease in the third week when oviposition begins, and their rate falls then below that of males (Riehl 1943).

Data of Butler and Innes show, further, very significant differences in the rate of respiration at the same temperatures between the solitary and the gregarious phases of locusts.

The influence of air humidity on the rate of respiration has been studied by Koidzumi (1934–35) and Ludwig (1937), and both authors arrived at the conclusion that this factor has practically no influence on respiratory metabolism.

8. *Water balance.*

Recent additions to our knowledge of water balance in ACRIDIDAE are few and to some extent contradictory. (For a summary of data and views on water balance in the terrestrial insects generally *see* Buxton 1932). Weed Pfeiffer (1945a) produced data on variations in water content of adult *Melanoplus differentialis* during its lifetime (fig. 18). Just after moulting to adult stage, percentage of water was higher in the males (76·4–77·7 per cent.) than in the females (72·8–75·3 per cent.) and tended to decrease more rapidly during the first period of the adult life which averaged 12 days. During the second period, the percentage water content remained fairly stable and differed little between the sexes, averaging on the 15th day, 66·2 per cent. in females and 67·8 per cent. in males. In females with corpora allata excised, a sharp reduction in water content was observed, parallel with an increase in fat content (p. 22, 41). Castration of females resulted in a great increase



18

Fig. 18.—Percentage of water (in terms of wet weight) in *Melanoplus differentialis*. -A, normal females; B, normal males; C, castrated females; D, females with corpora allata removed. (*After* Weed Pfeiffer 1945a.)

in water content and such females contained extremely large volumes of blood. Further discussion of the water and fat balance in relation to gonads should be best included in the summary on development.

Some data of interest were obtained by Millot & Fontaine (1937) in their experiments on *Schistocerca gregaria*. The average water content

of young adults was 71–76 per cent. of body weight, but considerable variations dependent on the air humidity were observed. The adult locusts placed immediately on emergence in a cage at 28° C. and 40 per cent. R.H., reduced their average water content after 6–8 weeks to 53 per cent. if they had fresh green food daily. If only dry food was given, the water content fell to 43 per cent. of body weight. In the locusts kept at 30° C. and 30 per cent. R.H. and given dry food, the water content was reduced to 37·4 per cent., while starving locusts after six days under the same conditions reached the record low figure of 36·5 per cent. This ability of *Schistocerca gregaria* to withstand a reduction in its water content to less than half the normal is very remarkable and may represent a physiological adaptation to the normal dry climate of its habitat. As a contrast, *Chorthophaga viridifasciata*, a North American grassland species, cannot survive if its water content falls below 56 per cent. of the body weight (Ludwig 1937).

The data of Millot and Fontaine suggest that food is the chief source of water but Ludwig's experiments (*l.c.*) showed that starving hoppers kept at an air humidity as low as 12 per cent. R.H., when the loss of water through evaporation must have been considerable, nevertheless maintained a high water content. This suggests (though does not prove), that the loss of water through evaporation may be compensated by an increased production, or retention, of metabolic water. Another point emerging from Ludwig's experiments was an increase in the water content of starving hoppers kept at high air humidity (over 80 per cent. R.H.), suggesting absorption of water from the air. Buxton (1932) suggested that it is not a purely physical phenomenon, but one involving condensation of atmospheric water in the tracheoles followed by its secretion from the liquid in the tracheoles into the body of the insect.

The problems connected with the loss of water through evaporation, or transpiration, were studied by Koidzumi (1934–35). The quantity of water per kilogram of body weight, lost in an hour by transpiration, varied considerably in different insects, and Table XIV shows the figures for three species of ACRIDIDAE, as compared with some other insects.

TABLE XIV.

Transpiration in different insects (after Koidzumi, modified).

Insect	Body weight in grams	Transpiration	
		Mg. per hour	Grms. per hour per kg. body weight
ACRIDIDAE			
Gastrimargus transversus ...	2·1345	22·3	10·447
Oxya vicina	0·7697	15·0	19·488
Acrida turrita	0·2933	3·8	12·956
HEMIPTERA			
Leptoglossus membranaceus ...	0·8615	14·2	16·482
LEPIDOPTERA			
Papilio demoleus	0·9504	27·9	29·368
HYMENOPTERA			
Polyrhachis dives	0·0611	6·3	103·109
COLEOPTERA			
Anomala expansa	1·3096	5·1	3·894

The table shows that the rate of transpiration in ACRIDIDAE may be described as medium in comparison with other insects, e.g. ants (*Polyrhachis*) which have a very much higher rate. Further, it is of interest that the Rice grasshopper (*Oxya vicina*) living near water has the transpiration rate twice as high as *Gastrimargus* or *Acrida* which live in relatively dry grassy habitats. It would be interesting to extend such determinations to ACRIDIDAE from many different habitats, in order to find out whether there is a physiological adjustment to the ecoclimate, or to the water content of food.

The mechanism of transpiration appears to be two-fold. Probably most important, from the quantitative point of view, is the loss of water vapour with the air exhaled through spiracles. Koidzumi made an attempt to investigate which of the spiracles are particularly concerned in transpiration, by covering their opening by a thin film of collodium, which is transparent in dry air but becomes cloudy on contact with water vapour. Observing that the first four pairs of spiracles showed particularly rapid clouding of the film, Koidzumi concluded that they play the main part in the transpiration, being expiratory in function. We have seen (p. 14) that this conclusion cannot be reconciled with other evidence on this point and the source of Koidzumi's error must have been in his method. Indeed, it is reasonable to suggest that the collodium film may become clouded under the influence of water vapour in the air inhaled through the spiracles, and not only in that exhaled. This possibility was not considered by Koidzumi and no experiments were made in dry air, when the source of the error would be minimised. However, this cannot affect the importance of respiration in reducing the water content of the organism.

By sealing all spiracles with vaseline and observing the amount of water vapour given out by the insect, Koidzumi claimed to have proved the existence of transpiration directly through the integument. The amount of water given out in this way was about one-fourth of the normal transpiration rate. Again applying the collodion method, Koidzumi found that transpiration occurs most actively through the thin intersegmental membranes of the abdomen, which was to be expected. Much more surprisingly, he was able to observe transpiration through the thick integument of the head capsule; this again throws doubt on the method used.

The influence of the air temperature on the total transpiration is very great, as would be expected, since a high temperature serves to increase both the direct evaporation of water from the body and the rate of respiration. According to Koidzumi's data, if the rate of transpiration at 10° C. is taken as a unit, transpiration at 20° C. would be 3·16, and at 30° C. would rise to 6·18 (always at 60 per cent. R.H.).

As regards the air humidity, its effects on transpiration are presented in Table XV, which shows that the loss of water at 90 per cent. R.H. is generally about half that at 30 per cent. R.H.

To conclude, the problem of water balance appears to be very complicated, owing to the strong conflicting influence on it of the various environmental factors (food, air humidity, temperature) and to the

ability of the insect to modify its water content by adjusting its respiratory rate, by absorbing water from the air and the food and perhaps by producing metabolic water. It is, therefore, scarcely possible to agree with Koidzumi's (*l.c.*) conclusion that transpiration from an insect body closely follows the law as of evaporation from a non-living object.

TABLE XV.

Relative rate of transpiration of *Gastrimargus transversus* at different humidities (after Koidzumi, modified).

°C.	% R.H.	Relative rate of transpiration.
10	30	1
	60	0·78
	90	0·55
20	30	1
	60	0·88
	90	0·50
30	30	1
	60	0·84
	90	0·55

9. *Heat metabolism*

Recent exact work on insect physiology tends to dispel the old ideas of insects as " cold-blooded " animals and to reveal the fact that their internal temperature[1], while dependent on that of the surrounding air, is subject to considerable changes due to other external factors and to physiological processes (see summary by Gunn 1942). These changes, in their turn, are of fundamental importance for the whole life of the insect, and particularly for its behaviour.

Measurements of the internal temperature are made by a needle thermocouple, the needle usually being introduced through the anus (Bodenheimer 1929a ; Koidzumi 1934-1935 ; Kennedy 1939). This, of course, causes some damage to internal organs and may affect the physiological state of the insect, but the results appear to be sufficiently accurate.

When studied in relation to the air temperature, the internal temperature of ACRIDIDAE is seldom identical with it. Usually, it is higher, the difference being sometimes as great as 10–15° C. ; the maximum difference so far observed was 26·7° C. (Krüger & Duspiva 1933). Under certain conditions, as will be seen later, the internal temperature may be lower than that of the air. Nevertheless, air temperature is certainly one of the most potent factors influencing the internal temperature.

[1] The usual term is " body temperature ", but since the latter may be measured on the surface of, as well as inside, the body, a more exact term, used by Volkonsky (1939), is adopted.

The process of adjustment of the internal temperature to that of the air has been studied by Bodenheimer (1929a) and by Koidzumi (1934–35). Both authors found that on the transference of an inactive Acridid from a low to a high temperature a new level of internal temperature is reached in 6–12 minutes. Indirect evidence of the adjustment of internal temperature to that of the air was also obtained in Hussein's (1937a) experiments on behaviour of locusts at different temperatures; larger hoppers exhibited slower reactions to temperature changes than smaller ones probably because they took more time to adjust their inner temperatures by heat conduction through their bodies. This time-lag of the internal temperatures behind that of the air is an important point to be kept in mind in studies on locust behaviour under changeable temperature conditions. Rapid fluctuations in air temperature may not have time to influence the internal temperature, the curve of which will be smoother than that of the air temperature, because the small changes recorded by the air thermometer produce no internal effect and the effect of the larger changes lags behind (Kennedy 1939).

Whereas warm-blooded animals produce heat metabolically, this source plays only a relatively small part in the heat economy of insects. In the case of resting insects, Bodenheimer (1929a) even insisted that their internal temperature is that of the environment. Koidzumi (1934–35), however, observed definite differences between the air temperature and that on the surface and inside the body of *Gastrimargus transversus* at rest (Table XVI).

TABLE XVI.

Differences between the temperature of air at various relative humidities and of *Gastrimargus transversus* at rest (after Koidzumi).

Air		Difference in °C	
°C.	R.H. %	Inside the body	On the surface of the body
10	30	− 0·47	− 0·32
	60	+ 0·63	+ 0·49
	90	− 1·28	+ 1·17
20	30	− 0·38	− 0·63
	60	− 0·44	+ 0·36
	90	+ 0·47	+ 0·44
30	30	− 1·52	− 1·80
	60	− 0·19	− 0·35
	90	+ 0·87	+ 0·64

The figures in the table certainly suggest that the temperature both inside and outside the body is very close to that of the air. Nevertheless, the agreement is never exact, and moreover the differences exhibit a regular and very suggestive correlation with air humidity and with the level of the air temperature. At 10° C. the temperature, both on the

surface and inside the insect, was consistently higher than that of the air, whatever its humidity. At 30° C., the insect was definitely cooler than the air, particularly when the latter was dry. Of course, it is impossible to assert that the excess of internal temperature over that of the air at low temperature was entirely due to metabolic processes, but this possibility cannot be ruled out. Unfortunately, it would be extremely difficult and perhaps impossible to study the metabolic heat production by direct calorimetric methods, and Koidzumi attempted instead to calculate the balance of heat energy produced and given off by *Gastrimargus*. He has based his calculations on the caloric value of oxygen consumed and carbon dioxide produced per kilogram of body weight in an hour. The resulting figures are presented in Table XVII as revised by Gunn (1942), but they must be regarded with caution.

TABLE XVII.

Heat balance-sheet of the grasshopper, *Gastrimargus transversus* (av. weight about 2g.). Quantities of heat are in g. cal. per kg. per hr. (Koidzumi 1935).

External temp. °C.	Rel. hum. %	A Metabolic heat produced	B Heat lost by evaporation	C Heat lost by radiation and conduction	D Unexplained balance A−(B+C)	Av. divergence from temp. of air °C.	
						Body cavity	Cuticle
10	30	3,100	3,090	0	+ 10	+ 0·47	+ 0·32
	60	3,240	2,410	170	+ 650	+ 0·63	+ 0·49
	90	3,840	2,000	400	+ 1,440	+ 1·28	+ 1·17
20	30	7,380	8,500	0	− 1,120	− 0·38	− 0·63
	60	7,490	7,500	0	− 10	+ 0·44	+ 0·36
	90	6,940	4,290	180	+ 2,470	+ 0·47	+ 0·44
30	30	14,080	17,220	0	− 3,140	− 1·52	− 1·80
	60	14,720	14,520	0	+ (200)*	− 0·19	− 0·35
	90	14,370	9,460	250	+ 4,660	+ 0·87	+ 0·64

* There seems to be an error in the author's table in this line. He puts − 367·42 here. His figures are given to 0·01 cal. and they are given here to the nearest 10 cal.

Metabolic production of heat as a result of muscular activity may be very considerable. Volkonsky (1939) observed a 5–7° C. rise in the internal temperature of locusts as a result of fluttering their wings. In Strelnikov's (1935) observations, the temperature inside the thorax of a *Locusta migratoria* making flying movements rose in two minutes from 27° C. to 37° C., obviously as the result of the work of the wing muscles, since inside the abdomen only 30·5° C. was reached in the same period. In marching hoppers of the same species, the difference between the temperatures in the thorax and in the abdomen averaged 2–3° C., while in one case it reached 6° C. The difference becomes less towards

the evening when the energy of marching decreases. These observations refute Bodenheimer's (1929a) contention that heat production by muscular movement has no practical effect on internal temperature.

However, undoubtedly the most important source of heat energy is the radiant energy of the sun. Fortunately, this problem has recently received a great deal of attention and some valuable data have been obtained.

The effects of the absorption of solar radiation on the internal temperature of *Locusta migratoria* is strikingly illustrated by fig. 19 (Strelnikov 1936). The figure shows that the internal temperature of a hopper in the shade fluctuated during the experiment between 27·6–28·1°C., following closely the changes in the air temperature. The internal temperature of another hopper exposed to direct sunlight rose during the first minute from 27·7° C. to 36° C., and after ten minutes

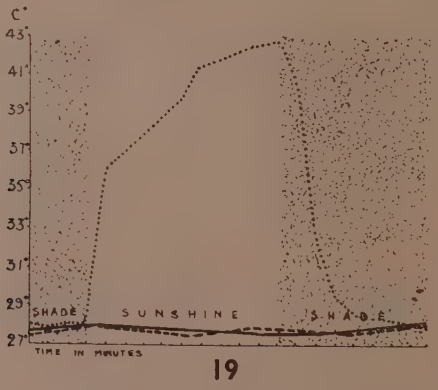


Fig. 19.—Effects of the absorption of solar radiation on internal temperature of *Locusta migratoria* hoppers.—Solid line, air temperature ; broken line, internal temperature of a hopper kept in shade throughout ; dotted line, internal temperature of a hopper shaded at first, then insolated, then shaded again. (*After* Strelnikov 1936, modified.)

of a less rapid rise it reached 42·7° C. When the hopper was shaded, its internal temperature fell in six minutes to that of the hopper kept continually in the shade.

Similar results were obtained by Bodenheimer with *Schistocerca gregaria* (1929a) and with a number of other ACRIDIDAE (1934) ; by Kennedy (1939) also with *S. gregaria ;* by Franz (1930) with *Oedipoda coerulescens ;* by Strelnikov (1932, 1935, 1936) with *Locusta migratoria ;* by the same author (1934) with *Sphingonotus savignyi* and *Thisoicetrus littoralis ;* by Krüger (1931) with *Gomphocerus sibiricus ;* and by Krüger and Duspiva (1933) with *Melanoplus frigidus* and *Podisma alpina.* In the case of the last named species, a record rise in the internal temperature by 26·7° C. over that of the air, as a result of insolation, was observed.

Strelnikov (1936) produced evidence that even dispersed radiation, from the sun covered by light clouds, may raise the internal temperature

of *Locusta* hoppers by 8·8° C. Heavier clouds act as a complete shade and the internal temperature follows closely that of the air. Reduction in solar radiation during desert dust-storms does not amount to complete shading and the temperature of *Thisoicetrus* and *Sphingonotus* was observed under these conditions to be about 5° C. above that in shade (Strelnikov 1934). Further data by Strelnikov (1936) suggest that the insolation of a portion of the body produces a rise of the internal temperature even in the unexposed parts, evidently as a result of conduction of heat through the body.

It is only to be expected that the angle at which heat rays strike the body should be an important factor in their absorption (Bodenheimer 1929a ; Strelnikov 1936 ; Volkonsky 1939 ; see Table XVIII).

TABLE XVIII.

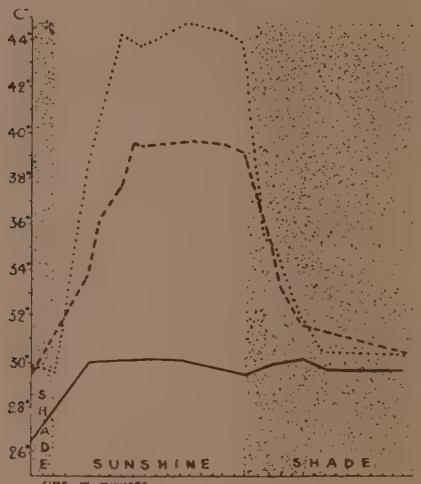
Internal temperatures in °C. of 5th stage hoppers of *Schistocerca gregaria* under the sun's rays falling at different angles (after Bodenheimer 1929a).

Relation of sun's rays to main axis of body		
At right angles	Parallel	Difference
38·7	35·7	3·0
42·1	38·2	3·9
45·1	41·6	3·5
45·1	42·5	2·6
38·9	36·0	2·9
40·2	36·0	4·2
Average 41·7	38·7	3·4

Strelnikov (1936) in his experiments on hoppers of *Locusta migratoria* obtained differences in the internal temperatures up to 6·7° C. depending on the angle of incidence of the sun rays. Volkonsky (1939) who has studied adults of the same species and of *Schistocerca gregaria*, observed that in the locusts sitting with their bodies parallel to the sun's rays, the internal temperature exceeded that of the air by 5·9–7·8° C., while in the locusts insolated by perpendicularly falling rays, the excess was 15·5–17·8° C. ; thus the angle of incidence of the sun's rays may cause a difference in the internal body temperature amounting to 10° C.

Since the absorption of heat rays is known to depend on the colour of the surface, the colouration of ACRIDIDAE is of special importance for the heat balance. This has been demonstrated by Buxton (*see* Uvarov 1928a) in the black and the buff colour forms of *Metromerus coelesyriensis*, the black one having the internal temperature 4–5° C. higher than the buff ; in Bodenheimer's (1934) experiments with the same grasshopper, the difference was 2–3° C. Hill and Taylor (1933) proved that the temperature under the pronotum in black gregarious hoppers of *Locusta migratoria* under an arc lamp and under direct sun was 3–3·5° C. higher

than in green solitary ones. Strelnikov (1936) made similar determinations under field conditions and found that the differences between internal temperatures of black (gregarious) and green (solitary) hoppers under identical conditions may be as much as 6·6° C. (fig. 20). The



20

Fig. 20.– Effects of colouration on the internal temperature of *Locusta migratoria* hoppers.— Solid line, air temperature; broken line, internal temperature of a green hopper (ph. *solitaria*); dotted line, internal temperature of a black hopper (ph. *gregaria*). (*After* Strelnikov 1936, modified.)

same author found a difference in the internal temperature of gregarious hoppers of the second and third stage; younger hoppers are darker and their temperature is higher by 1–2° C. than that of the third stage hoppers which are lighter in colour. One of Strelnikov's experiments suggests, further, that even differences in the colouration of various parts of the body may be of importance since in a hopper insolated dorsally the internal temperature rose 2·8° C. above that in another insolated ventrally, the ventral side being lighter coloured and with a smoother surface reflecting more rays.

The effect of the colour of the background (i.e. of the radiation reflected by it) on the internal temperature remains neglected. Some observations on the internal temperatures of *Oedipoda coerulescens* on white and black backgrounds by Franz (1930) were made under different conditions and are not comparable. Studies of this problem are greatly needed as they may throw light on the physiological significance of "sympathetic" colouration so common in ACRIDIDAE.

The above data indicate how varied are the sources of heat energy and how diverse their effects on the internal temperatures of ACRIDIDAE. The problem is, however, still further complicated by certain factors affecting the loss of heat by the organism.

Although, as we have just seen, the dark colouration favours the absorption of radiant energy, it is, on the other hand, a cause of a rapid loss of heat in the absence of insolation, since dark objects radiate heat at a greater rate than light coloured ones. This can be seen in the right hand portion of fig. 20 where the black gregarious hopper of *Locusta* in the shade cooled more rapidly than the green solitary hopper (Strelnikov 1936).

Again, energetic movement, such as flight, results in a rise of internal temperature, but on the other hand, this is accompanied by an increase in the rate of respiration (p. 16) and therefore in a better ventilation of the tracheal system. The air expelled from the tracheae is relatively warm and the loss of heat in this way must be considerable, while the quantity of cool air introduced into the body increases at higher temperatures. In addition, the air that is being expired carries out water vapour and a further cooling effect is produced by this evaporation through the spiracles. Strelnikov (1936) has demonstrated a considerable difference between the temperature in the thorax and inside the large thoracic air-sac of adult *Locusta migratoria*. Fig. 21 shows that, while the internal temperature rose under the influence of the sun's rays by 9° C. and exceeded the air temperature by 12·8° C., the temperature in the air-sac, although higher than that of the outer air, was well below the internal temperature. In another experiment, made in the shade,

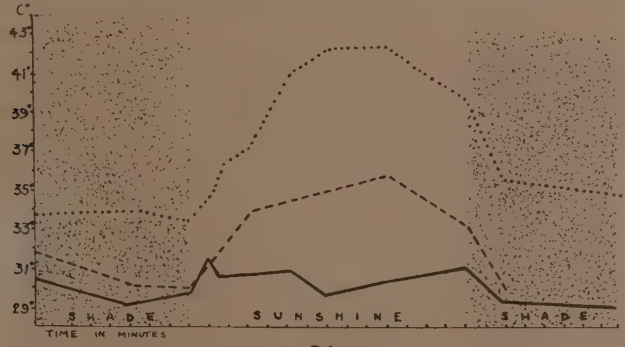


Fig. 21.—Temperature of adult *Locusta migratoria* taken inside the thorax (dotted line) and in the thoracic air-sac (broken line); solid line, outer air temperature. (*After* Strelnikov 1936, modified.)

the temperature in the air-sac was even below that of the outer air, which can be explained by the loss of heat in the course of evaporation.

The importance of the evaporation in the heat balance makes that balance dependent on the air humidity. Koidzumi (1934-1935) has shown that evaporation serves to delay the rise of internal temperature, and to speed up a fall; and both kinds of change depend on air humidity since it affects the rate of evaporation. In dry air, the temperature of *Schistocerca* (Bodenheimer 1929a) and of *Gastrimargus* (Koidzumi 1935) was 3–4° C. lower than in moist air. In the field, another important factor is introduced by air movements, even a slight breeze causing a fall in

internal temperature due to an increase in direct loss of heat and in evaporation from the body surface (Strelnikov 1936; Kennedy 1939).

Therefore, we see that heat metabolism is an extremely complicated process which has not yet received sufficient attention from insect physiologists, and that its result, the internal temperature, depends on a number of physiological and ecological factors. Moreover, some of these factors may have a varying effect, while the response of the organism to the same factor is not mechanical but subject to adjustment and variation. A simple mechanistic conception of heat balance is, therefore, grossly misleading. A further complication is introduced by the ability of an insect to effect a regulation of its internal temperature by behaviour reactions such as moving from one situation to another (e.g. from sun to shade), or even by merely altering its orientation to the sun's rays.

10. *Vitality.*

The lower vital limit of temperature in adults of *Schistocera gregaria* was found by Rungs (1933) to be under —5° C.; after an exposure to that temperature for about 12 hours the insects revived and behaved normally, but longer exposures often caused death. Bodenheimer (1929a, 1934) observed that at —14° C. the adults of the same species become frozen in 8–14 minutes, while in the first stage hoppers this happened at —10° C. in 1½ minutes, obviously owing to their smaller size. The average freezing point, measured as the internal temperature at freezing was —1·4° C. in the hoppers, —1·5° C. in the old adults and —0·9° C. in the young adults. In Rubtzov's (1935c) experiments, first stage hoppers of *Dasyhippus variegatus* survived exposures to —7° C. for 10 minutes, and were killed at —13·5° C. but the resistance of older hoppers was less and for the second stage hoppers the temperature of —12° C. was fatal, whereas the third stage hoppers were killed at —10° C. This grasshopper is the earliest to hatch in spring in Eastern Siberia, whereas first stage hoppers of *Arcyptera microptera*, which is a more thermophilous species, are killed at —7° C. That author remarks also that the resistance to low temperatures is reduced at greater humidity but gives no figures.

The lethal high internal temperature for adults of *Schistocerca gregaria* has been determined by Bodenheimer (1929a) as 51° C. Rubtzov (1935c) has established that external temperatures about 50° C. were lethal to five species of grasshoppers; in rare cases the limit was 54° C. Hussein's (1937) experiments with *Locusta migratoria migratorioides* have shown that the first stage hoppers became immobilised at 51·7° C., while in older hoppers and adults this happened at 55·6° C., and an exposure to these temperatures for 5–15 minutes resulted in death. If, however, the insects were removed immediately on reaching the limit, death did not occur until after some time, varying from one hour to three days. This shows the importance of the time of exposure, which is even better illustrated by observations on the first stage hoppers gradually heated to 48·3° C., and adults to 51·1° C.; these temperatures caused only a depression of activity and left no effect if the locusts were removed immediately; if, however, the exposure lasted for 1–2 hours, they ulti-

mately died. It should be noted that in these experiments the air humidity was kept between 65–80 per cent. and the lethal effects should not have been due to desiccation.

Desiccation as a sole cause of death has not been sufficiently studied, since the available data refer to observations on the combined effects of starvation and desiccation. Ludwig's (1937) results (Table XIX) suggest that, regardless of the initial water content, hoppers and adults of *Chorthophaga viridifasciata* can survive desiccation until their water

TABLE XIX.

Relation between the original water content and that at the time of death in *Chorthophaga viridifasciata* kept at 0–5% relative humidity (Ludwig 1937).

Stage	Water content in %		Weight at death as percentage of the original
	Original	At death	
Hibernating hoppers ...	65·6	56·1	72·5
Do. ...	68·1	58·8	72·4
Growing hoppers	70·7	56·3	61·1
Do. and adults ...	73·6	57·9	54·8
Do. do. ...	75·9	58·8	56·2

content averages 56·1–58·8 per cent. of the body weight. If the original water content is low, death results when only 28 per cent. of the original body weight has been lost ; if it is high, the insects survive a loss of more than 40 per cent. of the original weight. In the case of *Schistocerca gregaria*, the water content of starving adults can be reduced to 36·5 per cent. of the body weight without killing them (Millot et Fontaine 1937 ; *see* p. 49).

The effects of starvation were investigated by Bodenheimer (1929a) in *Schistocerca gregaria* (Table XX) and his data suggest a longer survival at higher air humidities. Observations on the loss of weight also showed that its rate was slower in humid air. Ludwig (1937) however, showed that the time for survival of starving hoppers of *Chorthophaga viridifasciata* and adults was the same, 5·2 to 6·6 days, regardless of the air humidity.

TABLE XX.

Length of life in days of starving *Schistocerca gregaria* at different relative humidities of air (Bodenheimer 1929a).

R.H. %	Hoppers			Old adults	Average
	2nd stage	3rd stage	5th stage		
0	4·4	4·1	1·0	2·0	2·9
20	1·0	2·7	1·8	3·0	2·1
40	3·0	5·3	1·5	3·0	3·2
60	3·4	5·5	3·0	4·8	3·9
80	1·5	6·1	2·5	3·0	3·4
100	3·5	4·7	3·0	5·8	4·5

Telenga (1930) in his starvation experiments with hoppers of *Schistocerca gregaria* obtained figures very different from those given by Bodenheimer. Hoppers of the first stage, kept without food or water, survived for two days ; those of the second and third stage, five days ; fourth stage, ten days ; and fifth stage, as long as fifteen days. The experiments have apparently been made in outdoor cages and the air humidity was not recorded. These figures approach the results obtained by Isely (1938b) who has kept fifteen different species of North American grasshoppers in open-air cages without food, but with water. First deaths occurred in two days, but some species of *Melanoplus* and *Hypochlora* survived from 12 to 14 days. From the taxonomic point of view it was of interest that members of the subfamily CATANTOPINAE were the most resistant to starvation, OEDIPODINAE took second place, and ACRIDINAE were the least hardy.

The diet appears to be another factor of some importance in survival of individuals. Females of *Melanoplus bivittatus* fed on a mixed diet survived, on the average, for 20·7–25·3 days after the beginning of oviposition (Drake, Decker & Tauber 1945), but the length of survival in females fed on different single foods varied widely (Tauber, Drake & Decker 1945). Thus females fed on mulberry shoots lived only 9·6 days ; those on castor oil plant and hemp and *Alopecurus pratensis* averaged 12–15 days ; on twelve plants the survival ranged from 16–20 days ; twelve plants showed results comparable to the average survival period on a mixed diet (21–25 days) ; and only two diets produced better results, viz. maize silk and shoots of cottonwood (*Populus deltoides*), on which the females survived for 27·1 days.

BIBLIOGRAPHY.

The following list contains titles of papers quoted in the present summary which are extracted from a full bibliography on all aspects of acridology, kept at the Anti-Locust Research Centre. Therefore, in case of several papers by an author bearing the same date there may be apparent gaps, e.g. SMITH 1929 may be followed by SMITH 1929b, which means that SMITH 1929a is a reference dealing with a subject outside the scope of this summary.

ADLER, E. *et al.*, 1934, Nutritive value of locusts. *Fmg. S. Afr.* **9** : 232.

AMOROSO, C., 1936, Sugli spiracoli tracheali degli Ortotteri. *Boll. Zool., Torino* **7** : 127–136, 4 figs.

ATHERTON, R. F., 1941, Visceral anatomy of two American lubber grasshoppers, with special reference to digestive and respiratory systems. *Univ. Colo. Stud.* **A26** : 128–130.

AUGER, D., and FESSARD, A., 1928, Recherches sur l'excitabilité du système nerveux des insectes. *C. R. Soc. Biol., Paris* **99** : 305–307.

AUGER, D., and FESSARD, A., 1928a, Observations sur l'excitabilité de l'organe tympanique du criquet. *C. R. Soc. Biol., Paris* **99** : 400–401.

AUGER, D., and FESSARD, A., 1929, Observations complémentaires sur un phénomène de contractions rythmées provoquées par excitation galvanique chez certains insects. *C. R. Soc. Biol., Paris* **101** : 897–899.

Beams, H. W., and King, R. L., 1932, Cytoplasmic structures in the ganglion cells of certain Orthoptera, with special reference to the Golgi bodies, mitochondria, "vacuome," intracellular trabeculae (trophospongium) and neurofibrillae. *J. Morph.* **53** : 59–96, 2 pls.

Beams, H. W. and King, R. L., 1932a, The architecture of the parietal cells of the salivary glands of the grasshopper, with special reference to the intracellular canaliculi, Golgi bodies and mitochondria. *J. Morph.* **53** : 223–242, 3 pls.

Beier, M., 1937, Eine neue Wehrdrüse bei saltatoren Orthopteren (Vorläufige Mitteilung). *C. R. Int. Congr. Zool. Lisbon* (1935) **12** : 1458–1462.

Bernard, F., 1937, Recherches sur la morphogenèse des yeux composés d'arthropodes. Développement, croissance, reduction. *Bull. biol. Suppl.* **23** : 172 pp., 6 pls., 20 figs.

Berretta, L., 1935, Genesi della membrana peritrophica nell' intestino degli Ortotteri. *Boll. Ist. zool., Palermo* **2** : 117–132, 2 pls.

———, 1937, La membrana peritrophica degli Ortotteri osservata in toto e origine di questa membrana. *Boll. Soc. Sci. nat. econ. Palermo* **19** : 5 pp., 2 figs.

Bickley, Wm. E., 1942, On the stomodaeal nervous system of insects. *Ann. ent. Soc. Amer.* **35** : 343–354, 2 figs., 2 pls.

Blumenthal, R. A., 1927, A micro blood sugar method and the blood sugars of insects. *Science* **65** : 617–619.

Boche, R. D., and Buck, J. B., 1942, Studies on the hydrogen-ion concentration of insect blood and their bearing on in vitro cytological technique. *Physiol. Zool.* **15** : 293–303.

Bodenheimer, F. S., 1929a, Studien zur Epidemiologie, Oekologie und Physiologie der afrikanischen Wanderheuschrecke (*Schistocerca gregaria*, Forsk.). *Z. angew. Ent.* **15** : 435–557, 55 figs.

———, 1934, Ueber die Temperaturabhängigkeiten der Insekten. IV. Ueber die Körpertemperatur der Insekten. *Zool. Jb.* (*Ab. I*) **66**: 113–151, 13 figs.

Boldyrev, V. F., 1929, Spermatophore fertilisation in the Migratory Locust (*Locusta migratoria*, L.). *Izv. prikl. Ent., Leningrad* **4** (1) : 189–218, 18 figs.

Broussy, J., 1933, Sur la nature et l'origine du pigment hypodermique d'*Anacridium aegyptium* (L.). *C. R. Ass. Anat.* **28** : 110–117, 2 figs.

Brown, A. W. A., 1937, Studies on the excreta of a grasshopper (*Melanoplus bivitattus* Say.). *J. exp. Biol.* **14** : 87–94.

———, 1937a, A note on the utilisation of polysaccharides by a grasshopper *Melanoplus bivittatus* Say. *Bull. ent. Res.* **28** : 333–336.

———, 1937b, A note on the chitinous nature of the peritrophic membrane of *Melanoplus bivittatus* Say. *J. exp. Biol.* **14** : 252–253.

Bruno, G., 1931, La cellula nervosa dei gangli cerebrali degli Ortotteri. *Boll. Soc. ital. Biol. sper.* **6** : 1001–1004.

Burtt, E. D., and Uvarov, B. P., 1944, Changes in wing pigmentation during the adult life of acrididae. *Proc. R. ent. Soc. Lond.* (A)**19** : 7–8, 3 figs.

Busnel, R. G., and Drilhon, A., 1942, Recherches sur la répartition de la riboflavine (Vitamine B_2) et de quelques autres substances fluorescentes chez les insectes. *Arch. Zool. exp. gén.* **82** : 321–356, 3 figs., 1 pl.

Butler, C. G., and Innes, J. M., 1936, A comparison of the rate of metabolic activity in the solitary and migratory phases of *Locusta migratoria*. *Proc. roy. Soc.* (B) **119** : 296–304, 3 figs.

Buxton, P. A., 1932, Terrestrial insects and the humidity of the environment. *Biol. Rev.* **7** : 275–320, 4 figs.

Carothers, E. E., 1939, A hybrid Acridian gynandromorph. *Genetics* **24** : 97.

Chang, K. F., 1931, The external anatomy of *Oedaleus marmoratus* Thunb. Part I. External anatomy of the head and mouthparts. *J. St. John's Sci. Soc. Shanghai* **1** : 15–38.

Chang, K. F., 1933, The external anatomy of *Oedaleus marmoratus* Thunb., Part 2: Exoskeleton of the thorax. *J. St. John's Sci. Soc., Shanghai,* **1** (2) : 40–79, 28 figs.

Chauvin, R., 1937, Les oenocytes du Criquet pèlerin (*Schistocerca gregaria* Forsk.). *C.R. Soc. Biol., Paris* **126** : 781–782.

———, 1938, Anatomie et histologie du tube digestif de *Schistocerca gregaria. Bull. Soc. Hist. nat. Afr. N.* **28** : 488–499, 4 pls.

———, 1938a, Morphologie et pigmentation externes de *Schistocerca gregaria* Forsk. (*transiens dissocians*). *Bull. Soc. Hist. nat. Afr. N.* **29** : 249–267, 4 figs.

———, 1938b, La respiration du criquet pèlerin *Schistocerca gregaria* Forsk. étudiée par la méthode graphique. *C. R. Coc. Biol., Paris* **128** : 1065–1067, 1 fig.

———, 1938c, Sur le rougissement du criquet pèlerin. *C. R. Acad. Sci., Paris* **207** : 1018–1020.

———, 1938d, Recherches histologiques sur les oenocytes du criquet pèlerin adulte *Schistocerca gregaria* Forsk. *Bull. Soc. Hist. nat. Afr. N.* **29** : 384–387, 1 pl.

———, 1938e, La réaction de Feulgen-Verne chez le criquet pèlerin. *C. R. Soc. Biol., Paris* **127** : 1075–1076.

———, 1939, Sur le pigment rose rejeté dans les excrements par le criquet pèlerin au moment de la mue. *C. R. Soc. Biol., Paris* **130** : 1194–1195.

———, 1939a, Influence du régime alimentaire sur le criquet pèlerin grégaire. *C. R. Soc. Biol., Paris* **131** : 31–33.

———, 1939b, Histologie du tégument chez le criquet pèlerin. *Bull. Histologie appliq., Lyon* **16** : 137–148, 5 figs.

———, 1939d, Sur quelque différences pigmentaires entre les criquets pèlerins grégaires et solitaires. *C. R. Soc. Biol., Paris* **132** : 397–398.

———, 1940, Nature et proprietés de l'acridioxanthine. *C. R. Acad. Sci. Paris* **211** : 339–340.

———, 1941b, Repartition de l'acridioxanthine chez les Orthoptères. *C. R. Soc. Biol., Paris* **135** : 334–335.

———, 1941c, Contribution à l'étude physiologique du Criquet pèlerin et du déterminisme des phénomènes grégaires. *Ann. Soc. ent. Fr.* **110** : 133–272, 23 figs.

———, 1944, Une nouvelle méthode d'appréciation de l'effet de groupe chez les Acridiens migrateurs. *Ann. Sci. nat. (Zool.)* (11) **5** : 79–87, 4 figs.

Chen, S. T., 1933, The chromosomes of some Peiping Orthopterans. *Peking nat. Hist. Bull.* **7** : 209–314, 1 pl.

Clark, E. J., 1943, Colour variation in British acrididae. *Ent. mon. Mag.* **79** : 91–104, 3 figs.

Creighton, M., and Robertson, W. R., 1941, Genetic studies on *Chorthippus longicornis. J. Hered.* **32**: 339–341, 1 pl.

Crescitelli, R., and Jahn, T. L., 1938, Electrical and mechanical aspects of the grasshopper cardiac cycle. *J. cell. comp. Physiol.* **11** : 359–376, 5 figs.

Crescitelli, F., and Jahn, T. L., 1939, The electrical response of the dark-adapted grasshopper eye to various intensities of illumination and to different qualities of light. *J. cell. comp. Physiol.* **13** : 105–112, 3 figs.

Crescitelli, F. and Jahn, T. L., 1939a, The effect of temperature on the electrical response of the grasshopper eye. *J. cell. comp. Physiol.* **14** : 13–27, 4 figs.

Crescitelli, F. and Jahn, T. L., 1942, Oscillatory electrical activity from the insect compound eye. *J. cell. comp. Physiol.* **19** : 47–66, 5 figs.

Das, S., 1945, Locust as food and manure. *Indian Farming, New Delhi* **6** : 412.

Debaisieux, P., 1937, Organes scolopidiaux des pattes d'insectes. *Cellule* **47** : 77–102, 12 pls., 28 figs.

Debauche, H., 1938, Les principaux organes sensoriels de l'antenne chez *Schistocerca gregaria* Forsk. *C.R.Ve. Conf. intern. Rech. antiacrid., Brussels* : 417–433, 4 pls.

Dehn, M. von, 1933, Untersuchungen über die Bildung der peritrophischen Membran bei den Insekten. *Z. Zellforsch.* **19** : 79–105, 12 figs.

Drake, G. J., Decker, G. C., and Tauber, O. E., 1945, Observations on oviposition and adult survival of some grasshoppers of economic importance. *Iowa St. Coll. J. Sci.* **19** : 207–223, 7 figs.

Drilhon, A., 1943, Sur la présence et l'activité des phosphatases chez les insectes. *C. R. Soc. Biol., Paris* **137** : 390–391.

Drilhon, A., et Busnel, R. G., 1939, Sur la présence et la teneur en flavine des tubes de Malpighi des insectes. *C. R. Acad. Sci., Paris* **208** : 839–841.

Duarte, A. J., 1939, On ecdysis in the African Migratory Locust [*Locusta migratoria migratorioides* R. & F.]. *Agronomia Lusitana, Lisbon* **1** : 22–40, 10 figs.

Eggers, F., 1928, Die stiftführenden Sinnesorgane. Morphologie und Physiologie der chordotonalen und der typanalen Sinnes-apparate der Insekten. *Zool. Baust.* **2** (1) : 354 pp., 149 figs.

Else, F. L., 1934, The developmental anatomy of male genitalia in *Melanoplus differentialis*. *J. Morph.* **55** : 577–610, 4 pls., 1 fig.

Faure, J. C., 1932, The phases of locusts in South Africa. *Bull. ent. Res.* **23** : 293–424, 25 pls., 1 map.

Fraenkel, G., 1932, Beiträge zur Physiologie der Atmung der Insekten. *Arch. zool., Torino* **16** : 905–921, 9 figs.

———, 1932a, Untersuchungen über die Koordination von Reflexen und automatisch-nervösen Rhythmen bei Insekten. I–IV. *Z. vergl. Physiol.* **16** : 371–462, 21 figs.

Franz, H., 1930, Untersuchungen über den Wärmehaushalt der Poikilothermen. *Biol. Zbl.* **50** : 158–182, 7 figs.

Friedrich, H., 1929, Vergleichende Untersuchungen über die tibialen Scolopalorgane einiger Orthopteren. *Z. wiss. Zool.* **134** : 84–148, 29 figs.

Friza, F., 1929, Zur Frage der Färbung und Zeichnung des facettierten Insektenauges. *Z. vergl. Physiol.* **8** : 289–336, 25 figs.

Gilmour, D., 1941, Repayment of the anaerobic oxygen debt in grasshopper skeletal muscle. *Biol. Bull., Woods Hole* **80** : 45–49.

Giral, F., 1941, Sobre aceites de insectos. I. *Taeniopoda auricornis*. *Rev. Soc. Mex. Hist. nat.* **2** : 243–250.

———, 1946, Grasas de insectos. V. *Sphenarium purpurascens* Charpentier. *J. biol. Chem.* **162** : 61–63.

Giral, J., Giral, F. and Giral, M. L., 1943, Sobre aceites de insectos. II. *Melanoplus sp. Ciencia, Mexico* **4** : 155–156

Giral, J., Giral, F. and Giral, M. L., 1944, Sobre aceites de insectos. III. Nuevos datos sobre *Taeniopoda auricornis* Walker. *Ciencia, Mexico* **4** : 215–216.

— ---, 1946, Grasas de insectos. IV. Composicion de la grasa de *Melanoplus atlanis* Riley. *J. biol. Chem.* **162** : 55–59.

Gourevitch, A., 1937, Sur le dosage de la flavine ; la flavine chez les invertébrés. *C. R. Soc. Chim. biol., Paris* **19** : 125–129.

Grayson, J. M., 1942, Studies of some factors influencing coloration of the grasshopper, *Melanoplus bivittatus* Say. *Iowa St. Coll. J. Sci.* **17** : 69–70.

Grayson, J. M., and Tauber, O. E., 1943, Carotin – the principal pigment responsible for variations in colouration in the adult grasshopper, *Melanoplus bivittatus* Say. *Iowa St. Coll. J. Sci.* **17** : 191–196, 1 fig.

Guarino, L., 1935, Osservazioni sull 'armatura genitale degli Acrididi. *Arch. zool. ital.* **21** : 427–446, 2 pls., 5 figs.

Guignon, G., 1936, Etude de la circulation sanguine des ailes chez les Coleoptères et les Orthoptères au moyen de la nicotine. *C. R. Acad. Sci., Paris* **202** : 2105–2106.

Gunn, D. L., 1942, Body temperature in poikilothermal animals. *Biol. Rev.* **17** : 293–314.

Hamilton, A. G., 1937, The mechanism of respiration of locusts and its bearing on the problem of inhalation of poison dusts. *Bull. ent. Res.* **28** : 53–68, 2 figs.

— –, 1937a, An abnormal mandible in the Desert Locust (*Schistocerca gregaria* Forsk.). *Proc. R. ent. Soc. Lond.* (A) **12** : 53–54, 1 fig.

Hamilton, A. G., and Milnthorpe, W. M., 1936, On an abnormality of the eighth abdominal segment in females of *Locusta migratoria* L. *Proc. R. ent. Soc. Lond.* (A) **11** : 29–32, 6 figs.

Hamilton, H. L., 1939, The action of acetylcholine, atropine and nicotine on the heart of the grasshopper (*Melanoplus differentialis*). *J. cell. comp. Physiol.* **13** : 91–103, 2 figs.

Hanström, B., 1936, Ueber eine Substanz im Insektenkopf, die zusammenballend auf das Pigment der Garneelen-Chromatophoren wirkt. *K. fysiogr. Sallsk. Lund Förh.* **6**(8) : 5 pp.

Hanström, B., 1938, Zwei Probleme betreffs der hormonalen Lokalisation im Insektenkopfe. *Acta Univ. Lund.* (2)**34**(16) : 17 pp., 6 figs.

Hanström, B., 1939, *Hormones in invertebrates.* Oxford, 198 pp., 13 pls.

Hanström, B., 1940, Inkretorische Organe, Sinnesorgane und Nervensystem des Kopfes einiger niederer Insektenordnungen. *K. svenska VetenskAkad. Handl.* **18**(8) : 266 pp., 239 figs.

Hanström, B., 1940a, Die chromatophoraktivierende Substanz des Insektenkopfes. *Acta Univ. Lund.* (N.S.) **36**(12) : 20 pp., 7 figs.

Hartline, H. K., 1928, A quantitative and descriptive study of the electric response to illumination of the arthropod eye. *Amer. J. Physiol.* **83** : 466–483, 4 figs.

Hastings, E. B., and Pepper, J. H., 1943, Studies on body fluids of seven Orthopterans, their pH, buffering capacity and effect on solubility of fractionated insecticides. *J. econ. Ent.* **36** : 857–864, 4 figs.

Heberdey, R. F., 1931, Zur Entwicklungsgeschichte, vergleichenden Anatomie und Physiologie der weiblichen Geschlechtsausführwege der Insekten. *Z. Morph. Okol. Tiere* **22** : 416–586, 85 figs.

Henry, G. M., 1942, Three remarkable stridulatory mechanisms in ACRIDIDAE. *Proc. R. ent. Soc. Lond.* (A) **17** : 59–62, 2 figs.

Herber, E. C., and Slifer, E. H., 1928, The regularity of respiratory movements of Locustidae. *Physiol. Zool.* **1** : 593–602, 9 figs.

Hers, J., 1938, Organe tympanal du *Schistocerca gregaria* Forsk. *C.R.Ve Conf. intern. Rech. antiacrid., Brussels* : 434–445, 2 pls.

Hertz, M., and Imms, A. D., 1937, On the responses of the African Migratory Locust (*Locusta migratoria migratorioides*, R. & F.) to different types of background. *Proc. roy. Soc.* (B) **122** : 281–297, 3 figs.

Hiestand, W. A., 1932, A comparison of the metabolic rates of various insects as determined by carbon dioxide output. *Proc. Ind. Acad. Sci.* **41** : 441–444.

Hill, L., and Taylor, H. J., 1933, Locusts in sunlight. *Nature* **132** : 276.

Hodge, C., 1936, The anatomy and histology of the alimentary tract of the grasshopper *Melanoplus differentialis* Thomas. *J. Morph.* **59** : 423–434, 2 pls.

Hodge, C., 1937, Some effects of diet on the gastric epithelial cells of the grasshopper, *Melanoplus differentialis* Thomas. *Biol. Bull. Wood's Hole* **72** : 203–211.

Hodge, C., 1939, The anatomy and histology of the alimentary tract of *Locusta migratoria* L. *J. Morph.* **64** : 375–400, 4 pls.

Hodge, C., 1940, The anatomy and histology of the alimentary tract of *Radenotatum* (*sic*!) *carinatum* var. *peninsulare* Rehn and Hebard. *J. Morph.* **66** : 581–604, 4 pls.

Hodge, C., 1943, The internal anatomy of *Leptysma marginicollis* (Serv.) and of *Opshomala vitreipennis* (Marsch.). *J. Morph.* **72** : 87–124, 4 pls.

Hollande, A. C., 1940, Solènosomes et chondriome de la cellule intestinale du criquet egyptien (*Orthacanthacris aegyptia* L.). Processus d'assimilation et coloration vitale. *C. R. Soc. Biol., Paris* **134** : 242–245, 1 fig.

—— –, 1943, Observations sur la structure du protoplasme et l'organisation de la cellule. *Arch. Zool. exp. gen.* **83** : 270–412, 36 figs., 6 pls.

Hubbell, T. H., and Cantrall, I. Y., 1938, A new species of *Appalachia* from Michigan. *Occ. Pap. Mus. Zool. Univ. Mich.* **389** : 22 pp., 1 pl.

Hussein, M., 1937a, The effect of temperature on locust activity. *Bull. Minist. Agric. Egypt* **184** : 55 pp., 3 figs., 22 graphs.

Ichikawa, Ch., 1936, Biochemical studies on the locust (1st Note). *J. agric. chem. Soc. Jap.* **12**(5) : 408–411.

Ichikawa, Ch., 1936a, Biochemical studies on the locust (2nd Note). *J. agric. chem. Soc. Jap.* **12**(5) : 412–414.

Ichikawa, Ch., 1937, Biochemical studies on the locust (3rd Note). Differences in the chemical constituents between two sexes. *J. agric. chem. Soc. Jap.* **13**(8) : 710–712.

Ichikawa, Ch., 1938, Biochemical studies on the locust (4th Note). Differences in the proteins between two sexes. *J. agric. chem. Soc. Jap.* **14**(1) : 43–44.

Imms, A. D., 1940, On growth processes in the antennae of insects. *Quart. J. micr. Sci.* **81** : 585–593, 1 fig.

Inafu, S., 1936, On *Oxya*. *Insect World, Gifu* **40** : 9–16. [In Japanese.]

Isely, F. B., 1938b, The relations of Texas acrididae to plants and soils. *Ecol. Monogr.* **8** : 551–604, 7 figs.

Isely, F. B., 1944, Correlation between mandibular morphology and food specifity in grasshoppers. *Ann. ent. Soc. Amer.* **37** : 47–67, 4 figs.

Itikawa, T., 1940, Biochemistry of the locust. *Nat. Sci. & Mus. Tokyo* **11**(7) : 4–11. [In Japanese.]

Jahn, T. L., and Crescitelli, F., 1938, The electrical response of the grasshopper eye under conditions of light and dark adaptation. *J. cell. comp. Physiol.* **12** : 39–55.

Jahn, T. L., and Crescitelli, F., 1940, Diurnal changes in the electrical response of the compound eye. *Biol. Bull. Wood's Hole* **78** : 42–52, 3 figs.

Jahn, T. L., Crescitelli, F., and Taylor, A. B., 1937, The electro-cardiogram of the grasshopper (*Melanoplus differentialis*). *J. cell. comp. Physiol.* **10** : 439–460, 8 figs.

Jahn, T. L., and Wulff, V. J., 1942, The effect of temperature on the retinal action potential. *Anat. Rec.* **84** : 535.

Jahn, T. L., and Wulff, V. J., 1942a, Allocation of electrical responses from the compound eye of grasshoppers. *J. gen. Physiol.* **26** : 75–88.

Jannone, G., 1938a, Osservazioni sulla presenza, struttura e funzione d'une vescicola ghiandolare confinata nel protorace delle specie mediterranee del gen. *Acrotylus* Fieb., con particolare riguardo all' *A. insubricus* (Scop.). *Boll. Lab. Zool. Portici* **31** : 41–62, 6 figs.

Jannone, G., 1939, Sulla diffusione della vescicola ghiandolare protoracica negli Ortotteri della subfam. oedipodinae. *Boll. zool. Torino* **10** : 1–3.

Jannone, G., 1939e, Studio morphologico, anatomico e isotologico del *Dociostaurus maroccanus* (Thunb.) nelle sue dasi *transiens congregans*, *gregaria* e *solitaria*. *Boll. Lab. Ent. agr. Portici* **4** : 1–443, 150 figs.

Jorg, M. E., 1933, Las terminaciones nerviosas musculares de *Elaeochlora viridicata*. *Rev. chil. Hist. nat.* **37** : 174–179, 5 figs.

Karandikar, K. R., 1939, External structures of the Desert Locust (*Schistocera gregaria*, Forsk.). *J. Univ. Bombay* **7** : 56 pp. 52 figs. [Separate reprint.]

Karandikar, K. R., 1942, External structures of the Desert Locust (*Schistocerca gregaria*, Forsk.). *J. Univ. Bombay* (*N.S.*) **11B**(3) : 1–29, 52 figs,

Kennedy, J. S., 1939, The behaviour of the desert locust (*Schistocerca gregaria*) (Forsk.) in an outbreak centre. *Trans. R. ent. Soc. Lond.* **89** : 385–542, 9 pls., 37 figs.

Kleinman, L. W., 1934, The effect of temperature upon the respiratory quotients of nymphs of the grasshoppers, *Chorthophaga viridifasciata* De Geer, and the larvae of the Japanese beetle *Popillia japonica* Newman, with reference to changes during hibernation. *J. cell. comp. Physiol.* **4** : 221–235, 1 fig.

Knetsch, H., 1939, Die Korrelation in der Ausbildung der Tympanalorgane, der Flügel, der Stridulationsapparate und anderer Organsysteme bei den Orthopteren. *Arch. Naturgesch.* (N.F.) **8** : 1–69, 70 figs.

Koidsumi, K., 1934–35, Experimentelle Studien über die Transpiration und den Wärmehaushalt bei Insekten. *Mem. Fac. Sci. Agric. Taihoku* **12**(1) : 1–179, 24 figs. ; **12**(3) : 281–336, 5 figs.

Korigawa, K., 1934, Chemical studies on the locust (1st Report). General analysis and protein. *Zyozogaku Zassi, Osaka* **12**(5) : 361–365.

Korigawa, K., 1934a, Chemical studies on the locust (supplemental note for 1st Report). Prolamine isolated from the locust. *Zyozogaku Zassi, Osaka* **12** : 445.

Kozhantschikow, I. W., 1934, Zur Frage nach dem Temperaturoptimum des Lebens. *Z. angew. Ent.* **20** : 590–610, 4 figs.

Kreps, E. M., and Chenykaeva, E. J., 1942, On the respiratory function of the blood of insects. *C. R. Acad. Sci. U.R.S.S.* **34** : 142–145.

Kreps, E. M., and Chenykaeva, E. J., 1942a, New data on the CO_2 exchange in Crustacea and insects. *Bull. Acad. Sci. U.R.S.S.* **1942** (no. 5) : 310–321.

Krüger, P., 1931, Weitere Beiträge über die Faktoren des Wärmehaushaltes der Poikilothermen. *Z. Morph. Okol. Tiere* **22** : 759–773, 3 figs.

Krüger, P., and Duspiva, F., 1933, Der Einfluss der Sonnenstrahlung auf die Lebensvorgänge der Poikilothermen. *Biol. gen.* **9** : 168–188, 7 figs.

Kunasheva, K. G., 1932, Determination of carbon in some species of acrididae. *Trav. Lab. biogéochim. U.R.S.S.* **2** : 27–30. [In Russian.]

Laird, A. K., 1943, A study of the types of male gonads found in the acrididae. *J. Morph.* **72** : 477–490, 4 figs.

Lapique, M., 1942, Détermination de chronaxie de quelques muscles d'insectes. *C. R. Soc. Biol., Paris* **136** : 298–300.

LAPP, C., et ROHMER, J., 1937, Composition et valeur alimentaire du Criquet pèlerin. *Bull. Soc. Chim. biol., Paris* **19** : 321–324, 2 figs.

LEDERER, E., 1934, Sur les caroténoids des téguments de quelques insectes. *C. R. Soc. Biol., Paris* **117** : 413–416.

LEDERER, E., 1938, Sur les caroténoides des invertébrés. *Bull. Soc. Chim. biol., Paris* **20** : 567–610.

LEE, M. O., 1929, The function of the air sacs in holopneustic insects. *Science* **69** : 334–335.

LEPESME, P., 1938, Note preliminaire sur la cytologie du sang des acridiens. *Bull. Soc. Hist. nat. Afr. N.* **29** : 241–248, 5 pls.

LERMA, B. de, 1937, Osservazioni sul sistema endocrino degli Insetti (corpora allata e corpori faringei). *Arch. Zool. ital., Torino* **24** : 339–368, 17 figs.

LISON, L., 1937, Etudes histophysiologiques sur le tube de Malpighi des insectes. I. Elimination des colorants acides par le tube de Malpighi chez les Orthoptères. *Arch. Biol.* **48** : 321–360.

———, 1937a, Etudes histophysiologiques sur le tube de Malpighi des insectes. II. Phenomènes d'athrocytose dans le tube de Malpighi chez les Orthoptères. *Arch. Biol.* **48** : 489–512, 1 pl.

———, 1938, Les phenomènes d'athrocytose dans le tube de Malpighi chez les insectes. *Ann. Soc. zool. Belg.* **68** : 41–48.

LU, H. T., and CHEN, T. T., 1928, The anatomy of *Cyrtacanthacris flavicornis* (ACRIDIINAE). *Proc. nat. Hist. Soc. Fukien Univ.* **1** : 49–58, 2 pls.

LUDWIG, D., 1937, The effect of different relative humidities on respiratory metabolism and survival of the grasshopper *Chortophaga viridifasciata* De Geer. *Physiol. Zool.* **10** : 342–351, 2 figs.

MCARTHUR, J., 1929, An experimental study of the functions of the different spiracles in certain Orthoptera. *J. exp. Zool.* **53** : 117–128.

MCCUTCHEON, F. H., 1940, The respiratory mechanism in the grasshopper [*Dissosteira carolina*, L.]. *Ann. ent. Soc. Amer.* **33** : 35–55, 7, figs.

MCGOVRAN, E. R., 1931, A method of measuring tracheal ventilation in insects and some results obtained with grasshoppers. *Ann. ent. Soc. Amer.* **24** : 751–761, 2 figs.

MCGOVRAN, E. R., 1932, The effect of some gases on the tracheal ventilation of grasshoppers. *J. econ. Ent.* **25** : 271–276.

MACHT, D. I., 1937, Physiological studies of grasshopper extracts. *Amer. J. Physiol.* **119** : 368–369.

MAGNAN, A., and PERILLIAT-BOTONET, Ch., 1932, Sur le poids relatif des muscles moteurs des ailes chez les insectes. *C. R. Acad. Sci., Paris* **195** : 559–561.

MAKI, T., 1938, Studies on the thoracic musculature of insects. *Mem. Fac. Sci. Agric. Taihoku* **24**(1) : 1–344, 17 pls.

MARSHALL, W. G., 1945, The rectal sac of the red-legged grasshopper, *Melanoplus femur-rubrum* De Geer. *Ann. ent. Soc. Amer.* **38** : 461–471.

MATHUR, C. B., and SONI, B. N., 1937, Studies on *Schistocerca gregaria* Forsk. IX. Some observations on the histology of the blood of the Desert Locust. *Indian J. agric. Sci.* **7** : 317–325, 2 pls.

MATTHEE, J. J., 1945, Biochemical differences between the solitary and gregarious phases of locusts and noctuids. *Bull. ent. Res.* **36** : 343–371.

MEANS, O. W., 1942, Cholinesterase activity of tissues of adult *Melanoplus differentialis*. *J. cell. comp. Physiol.* **20** : 319–324, 2 figs.

MELVIN, R., 1931, A quantitative study of copper in insects. *Ann. ent. Soc. Amer.* **24** : 485–488.

MILLOT, J., and FONTAINE, M., 1937, Etudes physiologiques sur les Orthoptères. I. La teneur en eau du criquet pèlerin adulte *Schistocerca gregaria* Forsk. *Bull. Soc. Hist. nat. Afr. N.* **28** : 412–418.

Millot, J., and Fontaine, M., 1938, Le taux de chitine chez *Schistocerca gregaria*. *Bull. Soc. zool.* **63** : 123–124.

Moxon, A. L., 1939, The selenium content of grasshoppers found feeding on seleniferous vegetation. *Proc. S. Dak. Acad. Sci.* **19** : 69–70.

Mukerji, S., and Batra, R. N., 1938, A note on the post-embryonic development of eye-stripes and their correlation with the number of larval instars and the antennal segments in the life-cycle of *Schistocerca gregaria* Forsk. *C.R.Ve Conf. intern. Rech. antiacrid., Brussels* : 410–416, 1 table.

Natori, B., 1931, On an ovo-testis found in a larva of locust *Podisma sapporoense* Shiraki. *Trans. Sapporo nat. Hist. Soc.* **12** : 1–5, 1 pl.

Nel, R. I., 1929, Studies on the development of the genitalia and the genital ducts in insects. I. Female of Orthoptera and Dermaptera. *Quart. J. micr. Sci.* **73** : 25–85, 3 pls. 5 figs.

Nelsen, O. E., 1934, The development of the ovary in the grasshopper *Melanoplus differentialis*. *J. Morph.* **55** : 515–544, 6 pls.

Nenyukov, D. V., and Parfent'ev, I. A., 1929, Digestive process and structure of intestine in the Migratory Locust. *Plant Prot., Leningrad* **6** : 21–37, 12 figs. [In Russian.]

Nesbitt, H. H. J., 1941, A comparative morphological study of the nervous system of the Orthoptera and related orders. *Ann. ent. Soc. Amer.* **34** : 51–71, 70 figs.

Newell, G. E., and Baxter, E. W., 1936, On the nature of the free cell-border of certain mid-gut epithelia. *Quart. J. micr. Sci.* **79** : 123–150, 7 figs., 1 pl.

Nielsen, E. T., 1943, X-Ray observations on the passage of food in Orthoptera. *Ent. Medd.* **23** : 255—272, 5 figs., 2 pls.

Nolte, D. J., 1939, A comparative study of seven species of Transvaal acrididae, with special reference to the chromosome complex. *J. ent. Soc. S. Afr.* **2** : 196–260, 144 figs.

Okay, S., 1945, Pigmentation of Orthoptera. *Nature* **155** : 635.

Olsen, R. F., 1943, The effects of transmitted colored light upon the pigmentation of grasshoppers. *Univ. Colo. Stud.* **27A**(2) : 27–28.

Paoli, G., 1937, Osservazioni su alcune particolarità di struttura e funzione dell' apparato genitale femminile di *Dociostaurus maroccanus* Thnb. (Orthopt. acrididae). *Redia* **23** : 17–26, 8 figs.

Paul, L. C., 1941, Intersexuality in *Camnula pellucida* Scudder. *Canad. Ent.* **73** : 195–196, 1 fig.

Payne, M. A., 1933, The structure of the testis and movement of sperms in *Chortophaga viridifasciata* as demonstrated by intravitam technique. *J. Morph.* **54** : 321–343.

Pfeiffer *see* Weed Pfeiffer.

Pilat, M., 1935, Histological researches into the action of insecticides on the intestinal tube of insects. *Bull. ent. Res.* **26** : 165–172, 4 pls.

———, 1935a, The effects of intestinal poisoning on the blood of locusts (*Locusta migratoria*). *Bull. ent. Res.* **26** : 283–288, 2 pls.

———, 1936, A histological study of the effect of insecticides on the alimentary canal of insects. *Bull. Pl. Prot., Leningr.* (3) **7** : 79–91, 20 figs. [In Russian.]

———, 1936a, Histological structure of blood of *Locusta migratoria* at poisoning with stomach insecticides. *Bull. Pl. Prot., Leningr.* (3) **7** : 92–99, 38 figs. [In Russian.]

Potter, E., 1940, A gynandromorph specimen of *Anacridium moestum* (Serv.). *Proc. R. ent. Soc. Lond.* (A) **15** : 41–46, 15 figs.

PREDTECHENSKII, S. A., 1935, Studies on the Desert Locust (*Schistocerca gregaria* Forsk.) in Central Asia and Transcaucasus in 1929–30. *Bull. Pl. Prot., Leningr.* (1 Ent.) **11** : 1–91, 6 figs. [In Russian.]

PRYOR, M. G. M., 1939, On the hardening of the cuticle of insects. *Proc. roy. Soc.* (B) **128** : 393–407, 5 figs.

PUMPHREY, R. J., 1940, Hearing in insects. *Biol. Rev.* **15** : 107–192, 10 figs.

PUMPHREY, R. J., and RAWDON-SMITH, A. F., 1936, Sensitivity of insects to sound. *Nature* **137** : 990, 1 fig.

PUMPHREY, R. J., and RAWDON-SMITH, A. F., 1936a, Hearing in insects : the nature of the response of certain receptors to auditory stimuli. *Proc. roy. Soc.* (B) **121** : 18–27, 2 pls., 2 figs.

PUMPHREY, R. J., and RAWDON-SMITH, A. F., 1939, Frequency discrimination in insects : a new theory. *Nature* **143** : 806–807.

QADRI, M. A. H., 1940, On the development of the genitalia and their ducts of Orthopteroid insects. *Trans. R. ent. Soc. Lond.* **90** : 121–175, 7 pls., 17 figs.

RAHMAN, K. A., 1935, On the labium of *Locusta migratoria* L. *Ent. mon. Mag.* **71** : 137–138, 1 fig.

RAO, R. Y., 1938b, *A report on the work done by the research staff under the research entomologist to the Imperial Council of Agricultural Research at Karachi during the year* 1937. Govt. Press, New Delhi : ii + 62 pp.

RAO, R. Y., and GUPTA, R. L., 1939, Some notes on eye-stripes in ACRIDIDAE. *Ind. J. agric. Sci.* **9** : 727–729.

RIEDEL, F. A., 1941, Visceral anatomy of two American lubber grasshoppers, with special reference to digestive and respiratory system. *Univ. Colo. Stud.* **26** : 128–130.

RIEDEL, F. A., 1946, Connective tissue pattern in the ventriculus of certain lubber grasshoppers. *Ann. ent. Soc. Amer.* **39** : 298–303, 2 pls.

RIEHL, L. A., 1943, Oxygen consumption at various temperatures by nymphs and adults of the grasshopper *Melanoplus differentialis* (Thomas). *Iowa St. Coll. J. Sci.* **18** : 80–83.

ROBERTS, H. R., 1941, A comparative study of the subfamilies of the ACRIDIDAE primarily on the basis of their phallic structures. *Proc. Acad. nat. Sci. Philad.* **93** : 201–246, 90 figs.

ROEDER, K. D., 1939, Synchronised activity in the optic and protocerebral ganglia of the grasshopper, *Melanoplus femur-rubrum*. *J. cell comp. Physiol.* **14** : 229–307, 3 figs.

———, 1940, The origin of visual rhythms in the grasshopper *Melanoplus femur-rubrum*. *J. cell. comp. Physiol.* **16** : 399–401.

ROGERS, E., 1929, The effect of temperature on the oxygen consumption of an insect *Melanoplus differentialis*. *Physiol. Zool.* **2** : 275–283, 2 figs.

ROONWAL, M. L., 1935, An abnormality in the *Boyou calicial* (female accessory glands) of the desert locust *Schistocerca gregaria*, Forsk. *Nature* **135** : 394–395.

———, 1936a, On the existence of two different types of striped eyes among solitary type specimens of the Desert Locust *Schistocerca gregaria* Forsk. *Curr. Sci.* **5** : 24, 2 figs.

———, 1937, Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reiche and Frm. (Orthoptera, ACRIDIDAE). II. Organogeny. *Philos. Trans.* (B) **227** : 174–244, 7 pls., 14 figs.

———, 1945a, Presence of reddish pigment in eggs and ovarioles of the Desert Locust, and its probable phase significance. *Nature* **156** : 19.

ROTMAN, M. N., 1929, Contributions to the study of the chitin of the migratory locust (*Locusta migratoria*, L.) in its different stages and phases. *Plant. Prot., Leningrad* **6** : 369–378. [In Russian.]

Rubtzov, I. A., 1934, Fertility and climatic adaptations in Siberian grasshoppers. *Bull. ent. Res.* **25** : 339–348.

Rubtzov, I. A., 1935, Phase variation in non-swarming grasshoppers. *Bull. ent. Res.* **26** : 499-524, 2 pls.

Rubtzov, I. A., 1935a, The changeability of the environment as a condition of outbreaks of the ACRIDIDAE. *Trud. Zasch. Rast. Vost. Sibiri* **2** (4) : 25–44. [In Russian.]

Rubtzov, I., 1935c, Regularities in the development and behaviour of Siberian ACRIDIDAE in connection with climatic factors. *Bull. Acad. Sci. U.R.S.S.* **1935** : 789–824, 2 figs. [In Russian.]

Rungs, C., 1933, Observations preliminaires sur la resistance au froid de *Schistocerca gregaria*, Forsk. *Rev. Path. veg.* **20** : 314–322.

Salfi, M., 1935, Ipognatismo ed oxycefalia negli Ortotteri. *Boll. Zool. Torino* **6** : 311–315, 3 figs.

Salfi, M., 1937, La membrana peritrofica osservata alla "luce di Wood". *Boll. Zool., Torino* **8** : 91–93.

Sansome, F. S., and La Cour, L., 1935, The genetics of grasshoppers : *Chorthippus parallelus*. *J. Genet.* **30** : 415–422, 2 pls.

Schlottke, E., 1937, Untersuchungen uber die Verdauungsfermente der Insekten. ii. Die Fermente der Laub- und Feldheuschrecken und ihre Abhängigkeit von der Lebensweise. *Z. vergl. Physiol.* **24** : 422–450, 4 figs.

Schumacher, J., 1937, Die Hörorgane unserer Heuschrecken und Grillen. *Mikrokosmos* **30** : 185–189, 8 figs.

Severin, H. C., 1943, A study of a gynandromorph of *Melanoplus mexicanus mexicanus* (Sauss.). *J. N.Y. ent. Soc.* **51** : 179–182, 1 pl.

Sian, F. J., 1935, Parolado de insekta anatomio. La externa anatomio de *Locusta migratoria*. *Insecto Interesa* **1** (2–3) : 52–58 ; (4) : 17–20 ; (6) : 24–28 ; (8) : 23–28. [In Chinese.]

Skrjabina, E., 1936a, Ph of the insect intestine and blood and its modification at poisoning by arsenic and fluorine compounds. *Bull. Pl. Prot., Leningr.* (3) **7** : 9–23, 5 figs. [In Russian.]

Slifer, E. H., 1935, Morphology and development of the femoral chordotonal organs of *Melanoplus differentialis* (Orthoptera, ACRIDIDAE). *J. Morph.* **58** : 615–637, 5 pls., 5 figs.

———, 1936, The scoloparia of *Melanoplus differentialis* (Orthoptera, ACRIDIDAE). *Ent. News* **47** : 174–180.

———, 1939, The internal genitalia of female ACRIDINAE, OEDIPODINAE and PAULINIINAE. *J. Morph.* **65** : 437–455, 1 fig., 7 pls.

———, 1940, The internal genitalia of female TRINCHINAE, BATRACHOTETRIGINAE, PAMPHAGINAE and PYRGOMORPHINAE. *J. Morph.* **66** : 175–196, 2 figs., 6 pls.

———, 1940a, The internal genitalia of female OMMEXECHINAE and CYRTACANTHACRIDINAE. *J. Morph.* **67** : 199–216, 1 fig., 12 pls.

———, 1940b, Variations in the spermatheca of two species of grasshoppers. *Ent. News* **51** : 1–3, 2 pls.

———, 1943, The internal genitalia of some previously unstudied species of female ACRIDIDAE. *J. Morph.* **72** : 225–237, 3 pls.

Slifer, E. H., and King, R. L., 1936, An internal structure in the CYRTACANTHACRINAE of possible taxonomic value. *J. N.Y. ent. Soc.* **44** : 345–348.

Slifer, E. H., and Uvarov, B. P., 1938, Brunner's organ ; a structure found on the jumping legs of grasshoppers. *Proc. R. ent. Soc. Lond.* (A) **13** : 111–115, 1 pl.

Snodgrass, R. E., 1928, Morphology and evolution of the insect head and its appendages. *Smithson. misc. Coll.* **81** (3) : 158 pp., 57 figs.

———, 1929, The thoracic mechanism of a grasshopper, and its antecedents. *Smithson. misc. Coll.* **82** (2) : 111 pp., 54 figs.
———, 1935, The abdominal mechanisms of a grasshopper. *Smithson. misc. Coll.* **94** (6) : 1–89, 41 figs.
———, 1935a, *Principles of insect morphology.* London, pp. 667, 319 figs.
———, 1936, Morphology of the insect abdomen. Part III. The male genitalia. *Smithson. misc. Coll.* **95** (14) : 96 pp., 29 figs.
———, 1937, The male genitalia of Orthopteroid insects. *Smithson. misc. Coll.* **96** (5) : 108 pp., 42 figs.
Solf, V., 1931, Reizphysiologische Untersuchungen an Orthopteren-muskulatur. *Zool. Jb., Abt.* 3. **50** : 175–264, 50 figs.
Strel'nikov, I. D., 1932, The effect of solar radiation and wind on the temperature of the body and the behaviour of the larvae of the locust *Locusta migratoria*, L. *Sborn. Vizra* **4** : 76–81, 2 graphs. [In Russian.]
———, 1934, Light as factor in animal ecology. I. Influence of solar radiation on the body temperature of some poikilothermic animals. *Bull. Inst. Sci. Leshaft* **17–18** : 313–372, 12 figs. [In Russian.]
———, 1935, Zur Frage über die Wärmeproduktion der Insekten infolge von Bewegungen und Sonnenbestrahlung. *Bull. Inst. Sci. Leshaft* **19** : 243–255.
———, 1936, Effect of solar radiation and micro-climate upon the body temperature and behaviour of the larvae of *Locusta migratoria* L. *Trav. Inst. zool. Acad. Sci. U.R.S.S.* **2** : 637–733, 16 figs. [In Russian.]
Stuart, R. R., 1935, The anatomy and histology of the Malpighian tubules and the adjacent alimentary canal in *Melanoplus differentialis*. *J. Morph.* **58** : 173–188, 3 pls., 2 figs.
———, 1935a, The development of the mid-intestine in *Melanoplus differentialis* (acrididae : Orthoptera). *J. Morph.* **58** : 419–438, 2 pls.
Swingle, M. C., 1931, Notes on digestion in seven species of insects. *Ann. ent. Soc. Amer.* **24** : 177–180.
———, 1931a, Hydrogen ion concentration within the digestive tract of certain insects. *Ann. ent. Soc. Amer.* **24** : 489–495.
Takata, R., and Korigawa, K., 1934, Chemical studies on the locust (2nd Report). Inorganic constituents and vitamins. *Jyozogakau Zassi* **12** (11) : 824–829.
Tareeva, A. I., and Nenyukov, D. V., 1931, Effect of poisons on the normal digestion and blood of *Calliptamus*. *Bull. Pl. Prot., Leningr.* **3** (1) : 39–49. [In Russian.]
Tauber, O. E., Drake, C. J., and Decker, G. C., 1945. Effects of different food plants on egg production and adult survival of the grasshopper, *Melanoplus bivittatus* (Say). *Iowa St. Coll. J. Sci.* **19** : 343–359.
Tauber, O. E., and Yeager, J. F., 1935, On total hemolymph (blood) cell counts of insects. I. Orthoptera, Odonata, Hemiptera and Homoptera. *Ann. ent. Soc. Amer.* **28** : 229–240.
Taylor, I. R., and Crescitelli, F., 1944, The electrical changes in response to illumination of the dark- and light-adapted eye in *Dissosteira carolina*. *Physiol. Zool.* **17** : 193–199, 6 figs.
Telenga, N. A., 1930, Biological observations on *Schistocerca gregaria*, Forsk. in Khoresm in 1929. *Izv. Khoresm. s.-kh. op. Sta. Moscow* **6** : 27 pp., 6 figs., I pl. [In Russian.]
Timon-David, J., 1930, Recherches sur les matières grasses des insectes. *Ann. Fac. Sci. Marseille.* (2) **4** : 29–207, 4 pls.
Trewithick, H, P., and Lewis, R. R., 1939, Fat from locusts. *Oil and Soap* **16** : 128.

Tsujimoto, 1929, Untersuchungen von Insektenöl Leuchtkäfer, Heuschrecken und Grillenöl. *J. Soc. chem. Ind. Japan.* [Original not seen: quoted after Timon-David, 1930.]

Uvarov, B. P., 1928a, *Locusts and grasshoppers. A handbook for their study and control.* London (Imperial Bureau of Entomology) pp. xiii + 352, 9 pls., 1 map, 118 figs.

Uvarov, B. P., 1943, The tribe Thrinchini of the subfamily Pamphaginae and the interrelations of the Acridid subfamilies. *Trans. R. ent. Soc. Lond.* **93**: 1–72, 73 figs.

Uvarov, B. P., and Thomas, J. G., 1942, The probable mechanism of phase variation in the pronotum of locusts. *Proc. R. ent. Soc. Lond.* (A) **17**: 113–118, 4 figs.

Uvarov, E. B., 1931, The ash content of insects. *Bull. ent. Res.* **22**: 453–457.

Varde, V. P., 1929, Contribution à l'étude morphologique et ethologique des Orthoptères acrididae. *Bull. Soc. zool. Fr.* **54**: 477–483, 4 figs.

———, 1934, The protrusible vesicles in cyrtacanthacrinae-acridiinae. *J. Univ. Bombay* **2** (5): 53–57, 5 figs.

Varley, G. C., 1939, Unusual methods of stridulation in a cicada (*Clidophleps distanti* Van D.) and a grasshopper (*Oedaleonotus fuscipes* Scud.) in California. *Proc. R. ent. Soc. Lond.* (A) **14**: 97–100, 2 figs.

Vinogradov, A. P., 1929, Sur la détermination de l'eau, du carbone et de l'azote dans les organismes (d'insectes). *Mem. Acad. Sci. Ukraine* (*Sci. phys. math.*) **11**: 145–156.

———, 1937, Manganese in insects (formicidae). III. *C. R. Acad. Sci. U.R.S.S.* **14**: 357–359.

Vinogradov, A., and Neustrueva, M., 1930, Le manganèse dans les insectes. *C. R. Acad. Sci. U.R.S.S.* **1930**: 127–132.

Volkonsky, M., 1938b, Stries oculaires et âges larvaires chez les Acridiens. *Arch. Inst. Pasteur Alger.* **16**: 523–532, 11 figs.

———, 1938c, Sur la formation des stries oculaires chez les Acridiens. *C. R. Soc. Biol. Paris*, **129**: 154–157, 4 figs.

———, 1939, Sur le photoakinèse des acridiens. *Arch. Inst. Pasteur Alger.* **17**: 194–220, 1 fig., 1 pl.

Vorontzovskii, P. A., 1928, On the question of homological ranges of colour variation in acrididae. *Bull. Orenburg Pl. Prot. Sta.* **1**: 27–39. [In Russian]

Voskresenskaja, A., 1936, Poison penetration through the intestine wall of insects. *Bull. Pl. Prot., Leningr.* (3) **7**: 25–39, 8 figs. [In Russian.]

Weed, I. G., 1936, Removal of corpora allata on egg-production in the grasshopper *Melanoplus differentialis*. *Proc. Soc. exp. Biol. N.Y.* **34**: 883–885.

———, 1936a, Experimental study of moulting in the grasshopper, *Melanoplus differentialis*. *Proc. Soc. exp. Biol. N.Y.* **34**: 885–886.

Weed Pfeiffer, I., 1939, Experimental study of the function of the corpora allata in the grasshopper, *Melanoplus differentialis*. *J. exp. Zool.* **82**: 439–461, 1 fig.

———, 1945, The influence of the corpora allata over the development of nymphal characters in the grasshopper *Melanoplus differentialis*. *Trans. Conn. Acad. Arts Sci.* **36**: 489–515.

———, 1945a, Effect of the corpora allata on the metabolism of adult female grasshoppers. *J. exp. zool.* **99**: 183–233, 6 figs.

Weiss, H. B., 1944, Insect responses to colour. *J. N.Y. ent. Soc.* **52**: 267–271.

Wever, E. G., 1935, A study of hearing in the sulfur-winged grasshopper (*Arphia sulphurea*). *J. comp. Psychol.* **20**: 17–20, 1 fig.

WHITFIELD, F. G. S., and WOOD, A. H., 1935. *An introduction to comparative zoology.* London, pp. 354, 141 figs.

WIGGLESWORTH, V. B., 1939, *The principles of insect physiology.* London, pp. 434, 316 figs.

WOODRUFF, B. H., 1933, Studies on the epithelium lining the caeca and midgut in the grasshopper. *J. Morph.* **55** : 53–80, 2 pls.

ZACWILICHOWSKI, J., 1934, Innervation et organes sensoriels des ailes du *Stauroderus biguttulus* (L.). *C. R. Acad. Cracovie* **1934** (5) : 5–6.

———, 1934a, Ueber die Innervierung und die Sinnesorgane der Flügel der Feldheuschrecke *Stauroderus biguttulus* (L.). *Bull. int. Acad. Cracovie* **1934** (B) (II) : 187–188, 1 pl.

INDEX TO SPECIES.

The index includes the genera and species of ACRIDIDAE mentioned in the text. The species are assigned to their correct genera, according to the latest taxonomic opinion, and not to those under which they may be quoted in the original papers. Names of the authors of species are given in the index only and not in the text.

Acanthacris ruficornis (Fabricius), 39
Acrida turrita (Linnaeus), 10, 25, 34, 37, 44, 45, 49, 50
Acrotylus, 7
adelogyrus, Melanoplus
aegyptium, Anacridium
alpina, Podisma
ambigua, Atractomorpha
americana, Schistocerca
Anacridium aegyptium (Linnaeus), 6, 8, 9, 10, 11, 13, 20, 22, 23, 24, 25, 28, 35, 36, 37, 42, 43, 44
Anacridium moestum (Serville), 37
annulicornis, Hieroglyphus
Appalachia arcana, Hubbell & Cantrall, 37
arcana, Appalachia
Arcyptera microptera (Fischer-Waldheim), 58
Arphia sulphurea (Fabricius), 19, 28
Arphia xanthoptera (Burmeister), 36, 37
Asiotmethis muricatus (F. Waldheim), 31
Atractomorpha ambigua (Bolivar), 8
Aulocara elliotti (Thomas), 37
auricornis, Taeniopoda

banian, Hieroglyphus
bicolor, Chorthippus
biguttulus, Chorthippus
bivittatus, Melanoplus
Brachystola magna (Girard), 4, 9, 14, 20

Calliptamus italicus (Linnaeus), 11, 12, 16, 18, 25, 36
Caloptenopsis, 25
Camnula pellucida (Scudder), 37
cariniventris, Phonogaster
carolina, Dissosteira
Catantops, 25
Charora, 32
Chondracris rosea (De Geer), 3
Chorthippus, 4
Chorthippus bicolor (Charpentier), 21, 22
Chorthippus biguttulus (Linnaeus), 24
Chorthippus longicornis (Latreille), 37
Chorthophaga viridifasciata (De Geer), 33, 46, 49, 59
Chromacris colorata (Serville), 36
Chrotogonus, 25, 27
Chrotogonus trachypterus (Blanchard), 36
cisti, Tmethis
citrina, Trimerotropis
coelesyriensis, Metromerus
coerulans, Sphingonotus
coerulescens, Oedipoda
Colemania sphenarioides, Bolivar, 25, 34, 36
colorata, Chromacris
concinnula, Orphulella
corallipes, Xanthippus
Cyrtacanthacris flavicornis (Fabricius)=*Chondracris rosea* (De Geer), 3
Cyrtacanthacris tatarica (Linnaeus), 25

Dasyhippus variegatus (Fischer-Waldheim), 58
Dericorys, 25
differentialis, Melanoplus
Dissosteira carolina (Linnaeus), 4, 5, 9, 12, 14, 15, 17, 19, 23, 46
Dociostaurus maroccanus (Thunberg), 3, 8, 27, 30, 31, 33, 36, 42

Elaeochlora, 24
elliotti, Aulocara
Euryparyphes flexuosus (Bolivar), 36
Euthymia, 4

fasciata, Morphacris
femur-rubrum, Melanoplus
flavicornis, Cyrtacanthacris
flexuosus, Euryparyphes
frigidus, Melanoplus

Gastrimargus marmoratus (Thunberg), 4, 5, 9
Gastrimargus transversus (Thunberg), 46, 49, 50, 51, 52, 53, 57
germanica, Oedipoda
Gomphocerus sibiricus (Linnaeus), 37, 54
gregaria, Schistocerca

Hemiacris, 4
hieroglyphicus, Poecilocerus
Hieroglyphus annulicornis (Shiraki), 37
Hieroglyphus banian (Fabricius), 25
Hypochlora, 60
hystrix, Prionotropis

italicus, Calliptamus

japonica, Oxya

Leptysma marginicollis (Serville), 4, 9
littoralis, Thisoicetrus
Locusta migratoria (Linnaeus), 3, 4, 5, 6, 8, 9, 10, 11, 12, 14, 18, 20, 21, 22, 23, 24, 28, 30, 34, 35, 39, 42, 43, 44, 45, 46, 47, 53, 54, 55, 56, 57, 58
Locustana pardalina (Walker), 34, 36, 42
longicornis, Chorthippus

maculipennis, Mermiria
magna, Brachystola
mancus, Melanoplus
marginicollis, Leptysma
maritima, Trimerotropis
marmoratus, Gastrimargus
maroccanus, Dociostaurus
Mecostethus grossus, 22
Melanoplus adelogyrus, Hubbel, 37
Melanoplus bivittatus (Say), 13, 19, 21, 39, 44, 45, 60
Melanoplus differentialis (Thomas), 8, 9, 15, 17, 19, 20, 21, 22, 25, 26, 30, 35, 40, 41, 43, 46, 47, 48
Melanoplus femur-rubrum (De Geer), 12, 19, 21, 36, 37, 39
Melanoplus frigidus (Boheman), 54
Melanoplus mancus (Smith), 33
Melanoplus mexicanus (Saussure), 19, 37, 42
Melanoplus spretus=*M. mexicanus*
Mermiria maculipennis (Bruner), 4
Mesambria, 32
Mesopsis, 4
Metromerus coelesyriensis (Giglio-Tos), 55
mexicanus, Melanoplus
mexicanum, Sphenarium
microptera, Arcyptera
microptera, Romalea
migratoria, Locusta
mimica, Paraidemona

miniata, Oedipoda
moestum, Anacridium
monticollis, Teratodes
Morphacris fasciata (Thunberg), 7
muricatus, Asiotmethis

Nomadacris septemfasciata (Serville), 40

Ocneridia, 37
Oedaleus, 6
Oedaleonotus, 33
Oedaleonotus phryneicus, 37
Oedipoda, 8
Oedipoda coerulescens (Linnaeus), 8, 25, 36, 54, 56
Oedipoda germanica (Latrielle), 44
Oedipoda miniata (Pallas), 44
Opshomala vitreipennis (Marshall), 9
Orphulella concinnula (Walker), 37
Oxya japonica (Willemse), 42
Oxya velox (Fabricius), 38 39, 40, 43
Oxya vicina (Brunner), 49, 50

Paracinema tricolor (Thunberg), 8
Paraidemona mimica (Scudder), 37
paranensis, Schistocerca
pardalina, Locustana
Patanga succincta, 25
Paulinia, 28
pellucida, Camnula
Phonogaster cariniventris Henry, 32
phryneicus, Oedaleonotus
Podisma alpina (Koller), 54
Podisma sapporensis Shiraki, 37
Poecilocerus hieroglyphicus (Klug), 8
Poecilocerus vittatus (Klug), 37
Prionotropis hystrix (Germar), 9, 27, 31
Psectrocnemus, 32
Psopha stridula (Linnaeus), 25
Pyrgomorpha, 25

Radinotatum, 4, 9, 21
Romalea microptera (P. Beauvois), 3, 9, 14, 20, 34
rosea, Chondracris
ruficornis, Acanthacris

sapporensis, Podisma
savignyi, Sphingonotus
scalaris, Stauroderus
Schistocerca americana (Drury), 12, 23
Schistocerca gregaria (Forskål), 4, 5, 6, 9, 10, 11, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 31, 34, 38, 39, 40, 42, 43, 44, 45, 46, 47, 48, 49, 54, 55, 57, 58, 59, 60.
Schistocerca paranensis (Burmeister), 3, 25, 42
septemfasciata, Nomadacris
sibiricus, Gomphocerus
Spathosternum, 25
sphenarioides, Colemania
Sphenarium mexicanum Saussure, 33
Sphingonotus, 55
Sphingonotus coerulans (Linnaeus), 25
Sphingonotus savignyi Saussure, 54
Stauroderus scalaris (Fischer-Waldheim), 37
Stenobothrus, 10, 12, 28, 44
stridula, Psopha
sulphurea, Arphia

Taeniopoda auricornis (Walker), 39, 42, 43
tatarica, Cyrtacanthacris
Teratodes monticollis (Gray), 37
Thisoicetrus littoralis (Rambur), 25, 54, 55
Tmethis, 33
Tmethis cisti (Fabricius), 31, 37
trachypterus, Chrotogonus
transversus, Gastrimargus
tricolor, Paracinema
Trimerotropis citrina, Scudder 37
Trimerotropis maritima (Harris), 37
turrita, Acrida

variegatus, Dasyhippus
velox, Oxya
vicina, Oxya
viridifasciata, Chorthophaga
vitreipennis, Opshomala
vittatus, Poecilocerus

xanthoptera, Arphia
Xanthippus corallipes (Haldeman), 33

Zonocerus